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Western Burrowing Owls (*Athene cunicularia hypugaea*) in Southeast Alberta: Juvenile Survivorship from Fledging to Migration, Effect of Tags, and Late-season Diets

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in

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DEDICATION

I dedicate this thesis to my father, George, who instilled in me both respect and wonder for nature, particularly thorough his many friendships with chickadees and robins, and to my mother, Mitzie, who equally instilled curiosity for wild critters through her entrenched apprehension of anything with more or less than two legs.

ABSTRACT

Because large proportions of immature birds raised to independence do not survive to breed, it is important to determine whether juvenile survival is limiting population growth. I tracked radio-tagged juvenile Western Burrowing Owls (*Athene cunicularia hypugaea*) in southeast Alberta from fledging until migration, and recorded higher juvenile survival than that found in two other studies in terminally declining Canadian populations. I also evaluated two styles of radio-tags, necklaces and backpacks, and determined that necklace style tags may negatively affect juvenile survival. Because late season and cohort specific diets are rarely studied, I tracked dispersing adults and juveniles, and dissected pellets collected at their diurnal roost burrows, to contrast prey use. I found that dietary heterogeneity between adults and juveniles resulted principally from differences in biomass of nocturnally active prey, such as rodents and ground beetles, and that juvenile diets were almost predominantly insectivorous. I suggest that previously documented increases in the use of invertebrates in the late season, relative to typical breeding season diets, could result from the addition of independently foraging juveniles into the population. I also recorded the first instance of the consumption of horsehair worms, and suggest tertiary effects on Burrowing Owls via reduced nutritional and caloric quality of infected prey. Lastly, I tracked juveniles to nocturnal foraging sites to contrast prey availability with random sites, and suggest that the high incidence of juvenile insectivory in this study resulted from strategic nocturnal foraging on terrestrial arthropods.

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Finally, I wish to acknowledge the absolute pleasure it has been endeavouring to see the world through the vibrant yellow eyes of these unique sentinels of the perpetually undervalued North American prairie ecosystem.

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CHAPTER 1

BURROWING OWL NATURAL HISTORY AND THESIS INTRODUCTION

INTRODUCTION

Quantifying wildlife survival probabilities and mortality sources is important to our understanding of population dynamics, and can guide conservation efforts by identifying particularly vulnerable cohorts or populations (Newton 1979). Because a large proportion of immature birds that survive to independence do not survive to breed (Lack 1946), it is particularly important to evaluate the survival probabilities of immature birds in declining populations. Measures of survivorship also enable comparative assessments of habitat quality (Anders et al. 1997) because animals generally have greater survival in higher quality habitats.

The North American Great Plains, the assemblage of central grasslands that historically encompassed 19% of the continent between southern Canada and northern Mexico (Figure 1-1), are now considered one of the most imperilled ecosystems on Earth, as a consequence of extensive native habitat and wildlife losses (Gauthier et al. 2003). Many prairie wildlife populations have become greatly reduced or extirpated, and, in recent decades, bird populations in the Great Plains have declined disproportionately relative to other North American bird groups (Herkert 1995, Peterjohn and Sauer 1999). The core of the Western Burrowing Owl (*Athene cunicularia hypugaea*) breeding range encompasses the Great Plains, and population declines and local extirpations have become apparent over the past few decades, notably in the eastern and northern periphery of the breeding range (Wellicome and Holroyd 2001). Extensive habitat destruction and degradation are the two most important factors influencing bird declines (Vickery et al. 1999). Assessing the potential relationship between survivorship and the effects of grassland loss in declining bird populations may provide insight into factors hindering population growth and recovery.

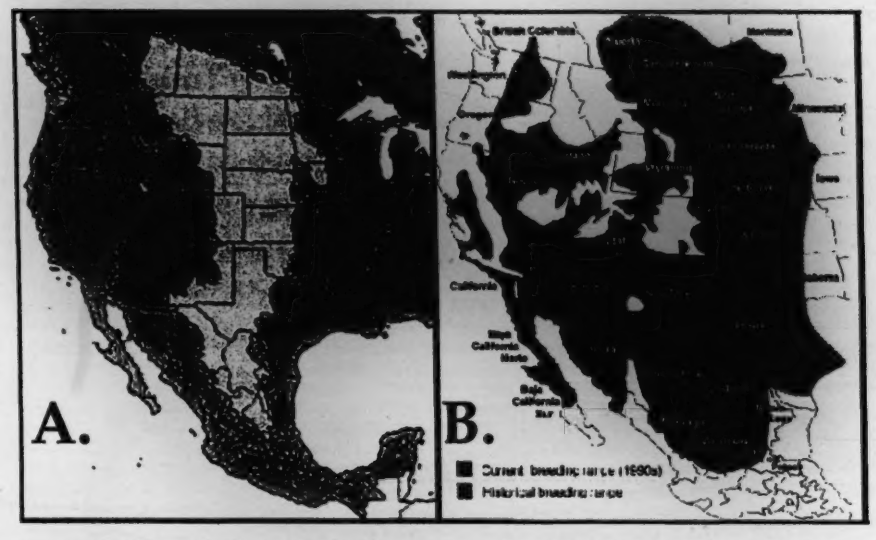

FIGURE 1-1. Historical extent (light grey) of the central Great Plains grasslands (A) in North America (modified from Wiken et al. 2002), and the historical and current breeding range (B) of the Western Burrowing Owl (modified from Wellicome and Holroyd 2001).

The widespread destruction and degradation of the North American grasslands have reduced the availability of suitable breeding, foraging, and migratory habitats for Burrowing Owls, resulting in diminished habitat quality and reduced population growth. Contemporary research provides evidence that grassland destruction and degradation are negatively impacting Burrowing Owl ecology and demography. For example, a greater proportion of mortalities are due to anthropogenic causes in agricultural habitats than in more contiguous native prairie (Clayton and Schumtz 1999) and survivorship is greater in larger (> 64 ha) rather than smaller remnant prairie patches (Todd et al. 2003). Furthermore, owls in small grassland patches disperse later, over shorter distances, and less often than those in more expansive grasslands (Clayton and Schumtz 1999). Habitat loss and fragmentation also affects breeding ecology by influencing nest site selection (Bothelo and Arrowood 1995, Millsap and Bear 2000, Moulton 2003, Orth and Kennedy 2001) and are negatively correlated with the persistence of breeding owls (Warnock 1997). Further, grassland habitat alterations can reduce prey availability (Moulton 2003, Poulin et al. 2001) and increase predator abundances, which can negatively impact owl survival. Although the

mechanisms by which land-use changes can detrimentally affect Burrowing Owl demography are becoming apparent, comparative research combining 1) demography in populations with disparate trends and 2) owl habitats with differing levels of native grassland retention, are required to better understand the relative importance of these habitat changes on population demography.

NATURAL HISTORY AND POPULATION STATUS

Three small owls constitute the genus *Athene*: the Burrowing Owl, distributed throughout the Americas; the Little Owl (*A. noctua*), inhabiting Europe and northern Africa through the Middle East to the Pacific coast of China; and the Spotted Owlet (*A. brama*), ranging south of the Little Owl distribution in the Middle East throughout the Indian sub-continent to the Pacific coast of South East Asia. *Athene* owls have similar plumage characteristics, are active both diurnally and nocturnally (i.e., cathemeral), have similar insectivorous/carnivorous diets consisting of small animals that are often considered pests by people (e.g., rodents and grasshoppers), are associated with open areas such as forest openings and prairie, and are obligate cavity nesters. Burrowing Owls are principally terrestrial rather than arboreal, and have the unique trait of principally nesting in subterranean cavities created by fossorial (i.e., burrowing) mammals rather than in elevated cavities.

There are 20 races of Burrowing Owl continentally distributed from southern Canada to southern Chile and Argentina, and on a few Caribbean and Pacific islands. The two North American races split ca. 350 000 years ago (Desmond et al. 2001); the resident Florida Burrowing Owl (*A. c. floridana*) now inhabits the Florida peninsula, while the migratory Western Burrowing Owl occurs in central and western North America from southern Canada to northern Central America (Haug et al. 1993). Western Burrowing Owl breeding range in Canada currently encompasses the northern Great Plains grasslands in Saskatchewan and Alberta.

Burrowing Owls in northern ranges are highly vagile, migrating from wintering areas in Texas and Mexico (G. Holroyd pers. comm.) to the Canadian prairie in April and May, where they attend natal territories until dispersal in July and August. Adult males provide food (primarily invertebrates and small rodents) to their incubating female partners, but once nestlings are sufficiently developed to independently thermoregulate, the adult female assists the male foraging for the brood. After fledging, adults and juveniles locally disperse from natal territories until the long-distance southward migration in September and October.

The population size and breeding range of the Florida subspecies increased as a consequence of large-scale deforestations in the northern and central areas of the peninsula (Courser 1979). In contrast, at least two Caribbean races have become extinct in historic times (Clark 1997) and populations of the Western subspecies (hereafter Burrowing Owl) have decreased to extirpation in British Columbia, Manitoba, Minnesota, and Iowa (Wellicome and Holroyd 2001), although a captive breeding and release program is achieving some success reintroducing the species to the south-central British Columbia cordilleran prairie (Leupin and Low 2001). In Alberta and Saskatchewan, the enduring core breeding range in Canada, landowner reports have documented terminally decreasing (> 90% reduction) populations (Wellicome 1997, Skeel et al. 2001). Two standardized surveys in southern Alberta over the past decade documented disparate population trends in similarly contiguous native prairie landscapes: a terminal trend in the northern periphery of the breeding range near the town of Hanna contrasts with a comparatively stable trend 150 km south near the town of Brooks (Shyry et al. 2001).

Burrowing Owls are considered a *Bird of Conservation Concern* in the United States (Klute et al. 2003), however, because of the persistence and pervasiveness of the population decline and extensive breeding range retraction, the population status is *Endangered* in Canada (COSEWIC 2003).

LIMITING FACTORS

There are numerous factors that contribute to Burrowing Owl population declines and inhibit recovery. Here I focus on the principal factors that have likely had the greatest influence: habitat destruction and degradation, prairie biodiversity change, and biocides.

Habitat Loss and Degradation

Habitat conversions, principally through the cultivation of grasslands to croplands, have dramatically reduced the extent of the Great Plains, and most native grassland now occurs in small patches surrounded by a cropland matrix. Owls in small patches may be subjected to detrimental fragmentation effects, such as increased predation rates or prey shortages that can limit reproductive success, and these fragmented habitats may act as 'sink' habitats, wherein mortality exceeds recruitment (Pulliam 1988).

In Canada, the once vast and contiguous prairies have been converted into a disconnected patchwork of refugia. For example, human activities have caused severe loss > 99% of the tall-grass prairie in Manitoba. Alberta retains the greatest proportion of native grasslands in Canada, but even in this province less than of native grasslands remain (http://www.albertapcf.ab.ca/index.htm). Remarkably, this 'sodbusting' in Alberta industriously occurred over the period of a single human life (60-70 yr). Although somewhat extensive and relatively contiguous grasslands abut the southern Alberta-Saskatchewan border, these areas are privately owned and subject to development if economic conditions become favourable, or if landowner priorities drift away from sustainable grazing. Indeed, government incentives have historically promoted the cultivation of native prairie, and there is currently very little native prairie habitat in Canada under legislative protection that would conserve this endangered habitat both for wildlife and for future generations.

Remnant prairie patches are becoming progressively more fragmented and degraded by agricultural conversion, petroleum industry developments, transportation corridors, urban sprawl, and novel and exotic species. The destruction of native prairie directly reduces the extent of suitable nesting, dispersal, and migratory habitats, and can reduce habitat quality if appropriate prey populations become reduced or predator populations increase. Because of the substantial and cumulative negative impacts of habitat loss on Burrowing Owls, habitat loss is considered the ultimate cause of population decline and breeding range retraction in Canada (Wellicome and Holroyd 2001).

Prairie Biodiversity Change

Wildlife Community Structure – Prairie wildlife community structure was irreversibly impacted by European settlement of the Great Plains. Many prairie herbivores (e.g., prairie dogs (*Cynomys* spp.), American bison and wapiti (*Cervus elaphus*)) and predator (e.g., black-footed ferret (*Mustela nigripes*) cougar (*Puma concolor*), plains grizzly (*Ursus arctos*), swift fox (*Vulpes velox*) and wolf (*Canis lupus*)) populations were decimated by excessive hunting and poisoning. Indeed, 73% of the wildlife species at risk in Alberta rely on prairie grasslands (http://www.albertapcf.ab.ca/index.htm). Such a substantial alteration of the wildlife community undoubtedly affects ecosystem function, and can impact Burrowing Owl ecology by affecting both predator and prey populations and by reducing the availability of suitable nesting habitat.

Prey Community – Beetles, grasshoppers, and small rodents, the principal prey of Burrowing Owls, can exhibit localized or epidemic population increases. The value of irruptive and cyclical prey cycles to Burrowing Owls is demonstrated by functional (i.e., increased nestling survival, fledgling success, post-fledging survivorship, and first-year recruitment) and numerical increases attributable to abundant small rodents (Haley 2002, Jaksic et al. 1997, Poulin et al. 2001, Silva et al. 1995, Todd et al. 2003, Wellicome 2000). In addition to grazing and biocides, the cultural elimination of prairie fires and filling > 75% of prairie wetlands also

may contribute to reduced prey availability and less frequent prey cycles. Reduced prey abundances or less frequent prey irruptions (e.g., the extinction of the Rocky Mountain Locust (*Melanoplus spretus*)) may limit Burrowing Owl population growth and recovery (see Poulin 2003).

Predator Community – The extirpated large prairie predator guild has generally been replaced by smaller predators such as coyotes (*C. latrans*), feral cats (*Felis catus*) and dogs (*C. familiaris*), raccoons (*Procyon lotor*), and red foxes (*V. vulpes*). Novel predators such as coyotes and exotic feral cats have been implicated in the death of individual owls and the failure of entire nests and colonies (e.g., Clayton 1997, Sleno 2000). Additionally, the nurturing of trees in farmyards and urban centers across the formerly treeless prairie expanses created habitats suitable for an influx of avian predators such as Red-tailed Hawks (*Buteo jamaicensis*) and Great-horned Owls (*Bubo virginianus*), that were formerly uncommon on the prairie (Houston and Bechard 1983, Kirk and Hyslop 1998). The presence of trees has been negatively correlated with Burrowing Owl nest success (Warnock and Skeel 2002) presumably because they attract raptorial predators and increase predation rates on the owls. While it is unknown if this novel predator community is responsible for inhibiting Burrowing Owl population growth, incidences of predation certainly diminish the potential for reproduction and recruitment.

Fossorial Mammals – While Burrowing Owls typically nest and shelter (roost) in burrows in prairie dog colonies, in the northern Great Plains where prairie dogs are absent they require ground squirrels (*Spermophilus* spp.) and badgers (*Taxidea taxus*) to create adequate subterranean cavities (Schmutz 1997). Because these owls are completely dependent on fossorial mammals, and these burrows are critically important for owl reproduction and survival (Coloumbe 1971, Desmond et al. 1995, Warnock and Skeel 2002), the elimination of fossorial mammals has been identified as a primary factor in recent and historical Burrowing Owl population declines (Klute et al. 2003). For example, the prairie

dog range is now reduced by > 98% (Cully and Williams 2001) due to aggressive control efforts and disease (Butts and Lewis 1982, Desmond et al. 2000). No similar documentation of ground squirrel or American badger distribution or population changes exists in the Canadian prairie despite ongoing persecution of these ecologically beneficial animals. Until the causes of fossorial mammal population and range reductions are reversed, the long term persistence of Burrowing Owls is likely in jeopardy.

Grazers – Contemporary prairie settlers have substituted resident cattle (*Bos taurus*) into the migratory bison's niche on remnant rangelands, which can increase grazing pressure on rangelands through increased stocking rates. Because Burrowing Owls select well-grazed natal territories with adequate burrows (Desmond and Savidge 1996, Schmutz 1997, Warnock and Skeel 2002), sustainable grazing of cattle is likely compatible with conservation efforts, but overstocking affects both small rodent (e.g., Birney et al. 1976, LoBue and Darnell 1959, Tait and Krebs 1983) and invertebrate (Capinera and Seachrist 1982, Onsager 2000) population dynamics which impacts owl survival and reproduction.

Biocides

The application of chemical pesticides near nests can affect Burrowing Owl survival and reproduction directly by poisoning owls that consume contaminated prey (Fox et al. 1989, James and Fox 1987) and indirectly by reducing prey availability. Thirty years after the dichlorodiphenyltrichloroethane (DDT) ban in Canada and the USA, metabolites such as dichlorodiphenyldichloroethylene (DDE) persist throughout North America and are responsible for impairing the reproduction of birds by critically thinning eggshells and reducing productivity. DDE has been found in Burrowing Owl feathers and eggs at elevated concentrations sufficient to impair reproduction and survival in other birds (Gervais et al. 2000, Gervais et al. 2003, Haug 1985). Burrowing Owl eggshells in California have thinned by 22% since 1937 (Gervais et al. 2000), but because

the evidence is circumstantial, it remains uncertain if DDE persistence and bioaccumulation impairs reproduction or survival of local and continental populations. Additionally, there is no published documentation of the pesticide loads of owls in Mexico, where DDT application was recently banned (in 2000).

Another insecticide for grasshoppers, Carbofuran, has restrictions limiting application to a distance > 50 m around owl nests in Canada (James and Fox 1987). The effectiveness of relying on product labelling to educate landowners about these restrictions is questionable (Mutafov 1992) relative to outright bans, and a 50 m buffer seems inadequate for a species that commonly forages 100's to 1000's of metres from the nest (Haley 2002, Haug 1985, Sissons 2003).

Because fossorial mammals are very infrequent prey of these owls, it is unlikely that chemical control of their populations will directly contaminate Burrowing Owls, but the poisoning of their populations has a secondary impact on owl reproduction by reducing nest burrow availability (James et al. 1990), which can contribute to population reductions and extirpations as a consequence of fossorial mammal eradications.

RESEARCH OBJECTIVES

Although many potential factors of Burrowing Owl population reductions and range retractions have been identified, the effect of these factors on owl demography remains elusive because of: 1) the dynamic nature of disturbances on the native prairie ecosystem (e.g., conversion and development, drought, fire, grazing), 2) the entrenched changes to prairie habitats and wildlife communities, 3) the vast distances and habitats traversed by northern owls during their life cycle, and 4) limited population-level research. Quantifying and evaluating the potential mechanisms limiting population growth are urgent because Burrowing Owl populations are being extirpated from their historical breeding range in Canada. It is important to conduct research on both natural history and demography before this species no longer inhabits these northern Great Plains, as

indicated by terminal population trends and local extirpations (e.g., British Columbia and Manitoba).

The relative effect of prairie habitat loss on Burrowing Owl populations can be assessed by contrasting demographic variables (e.g., survival and productivity) and natural history (e.g., prey utilisation) variables between populations residing in habitats with different levels of native prairie retention. Despite long-term demographic research in a terminally decreasing population in a landscape dominated by cereal crops (i.e., the Regina Plain, Saskatchewan), no similar long-term studies have been conducted in a population: 1) with a comparatively stable trend, or 2) residing in a landscape dominated by native prairie. Although food limitation is linked to increased mortality of immature owls (Todd et al. 2003, Wellicome 2000) only a single study has investigated post-breeding diets in the contracting northern limit of breeding range (Schmutz et al. 1991). Although radio-tags are commonly used in Burrowing Owl research, the potential impacts of these instruments has not been adequately assessed. Such research gaps limit the potential for investigating probable limiting factors, and preclude comprehensive comparisons of population demography between populations with dissimilar trends or residing in landscapes with different levels of breeding habitat retention.

I attempt to address some of these gaps in our understanding of Burrowing Owl demography and ecology at the northern limit of breeding range in southeast Alberta by investigating: 1) post-fledging survivorship (Chapter 3), 2) the effect of tag style on juvenile survival (Chapter 4), 3) juvenile prey use and availability in nocturnal foraging sites (Chapter 5), and 4) sex and age-specific late-season diets (Chapter 5). The data presented and discussed in this thesis was collected during the post-breeding period when the owls were dispersing away from natal territories (Figure 1-1). The University of Alberta's Animal Policy and Welfare Committee (http://www.afns.ualberta.ca/fapwc/) approved the field protocols for

this project each year. I provide additional information on each chapter, and a detailed description of the study area in the following sections.

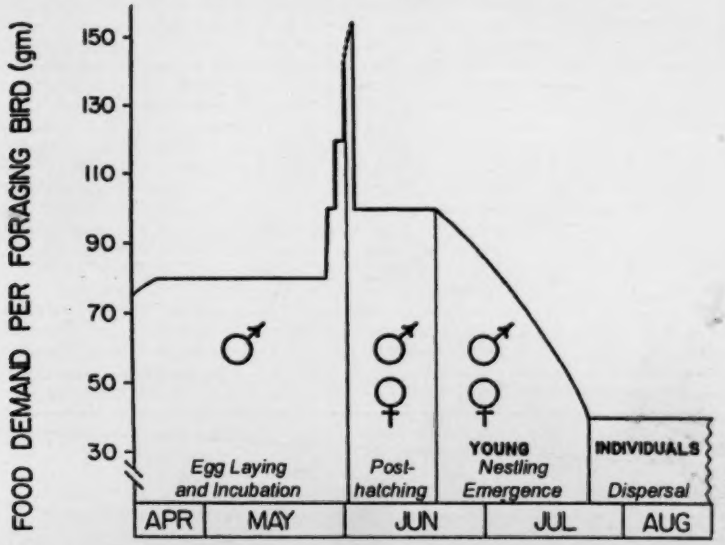

FIGURE 1-2. Variability in the breeding season food demands of a foraging owl from a hypothetical family group with four owlets. Intervals represent stages of breeding (*italics*) and the symbols and/or bold text in each interval indicate the owl(s) actively foraging. Research presented in this thesis was collected when owls are dispersing individuals (August – September). Figure adapted from Gleason (1978).

Juvenile Survivorship (Chapter 2)

Burrowing Owls are able to successfully breed when 1 yr old, therefore evaluating survivorship of juveniles (< 1 yr old) may provide insight into whether high mortality of immature birds is reducing recruitment and limiting population growth and recovery. Because standardised monitoring of the owl population near Brooks has revealed a comparatively stable trend over the past decade, I quantify post-fledging juvenile survivorship in this population to contrast with estimates from terminally decreasing populations near Hanna (Clayton 1997) and Regina (Todd 2001). I predicted that juvenile survival rates would be higher in the Brooks population. Additionally, because the extent and type of prairie habitat conversions can lead to higher rates of nest predation and parasitism, particularly near habitat edges (e.g., Johnson and Temple 1990, Winter et al.

2000), I predicted that survival rates and sources of Burrowing Owl mortality should be inverse to the proportion of native prairie habitat retention.

I tracked radio-tagged post-fledging juveniles until migration to assess survivorship in the Brooks population residing in relatively contiguous but linearly fragmented (e.g., roadways and pipelines) prairie. Subsequently, I contrasted survival rates and factors influencing survivorship with those presented in complementary and concurrent research from populations with terminally decreasing trends in: 1) a predominantly cultivated landscape that has experienced severe native grassland loss, near Regina (Clayton 1997, Todd 2001), and 2) similarly fragmented native prairie habitat, near Hanna (Clayton 1997).

Effect of Tag Style on Juvenile Survivorship (Chapter 3)

Although radio-tags can detrimentally affect survivorship, reproduction, and behaviour in some animals (see Calvo and Furness 1992 for a review), the potential impacts of tags have only been tentatively assessed in a few studies on Burrowing Owls. I investigated potential impacts of tags by comparing survivorship between pairs of siblings wearing two of the most common styles of tags used in Burrowing Owl research: 1) necklaces, and 2) backpacks.

Juvenile Prey Use and Availability in Nocturnal Foraging Sites (Chapter 4)

Investigating habitat and prey use of Burrowing Owls provides insight into causes of population reductions and contributes to the development of practical conservation strategies, but there are no published accounts of juvenile Burrowing Owl foraging habitat selection or prey utilisation. I tracked radio-tagged post-fledging juvenile owls to nocturnal foraging sites to assess prey use and availability. Specifically, I compared prey identified and enumerated in foraging sites with prey identified and enumerated in pellets (i.e., castings) collected at diurnal roosts.

Late-season Diets (Chapter 4)

Burrowing Owls consume a vast repertoire of prey that varies seasonally and geographically. Although the prey use of owls nesting in prairie dog towns is well documented, published diets in the northern breeding range where breeding habitat is defined by ground squirrel and badger burrows, are infrequent (Haug 1985, Schmutz et al. 1991, Sissons 2003). Additionally, although many researchers suggest that prey use is opportunistic, observations during breeding indicate sexual foraging disparity (Pezzolesi and Lutz 1997, Poulin 2003), implying that dietary specialization may be related to sex or stage of the breeding cycle (Silva et al. 1995). Only one post-mortem study has investigated diet disparity, and the results suggest that adult males have broader niche breadth during the breeding season than adult females (York et al. 2002). I tracked post-breeding adults and post-fledging juveniles to dispersal roost burrows where I collected regurgitated pellets and prey remains. Subsequently, I compared prey enumerated in these collections between adult male, adult female and juvenile cohorts, and contrasted prey used with other published late-season (i.e., post-breeding) diets.

STUDY AREA DETAILS & MAP

Historical Context

After the glaciers receded northward ca. 12 000 years ago, the Canadian prairies were a shifting mosaic of habitat patches created by the grazing activities of a diversity of abundant herbivores; wildfires ignited by lightening and aboriginals; and climactic extremes such as periodic and prolonged droughts, and severely cold winters. These factors have precluded tree growth onto the upland grasslands. For thousands of years, tribes of nomadic aboriginal plains peoples (e.g., Kainai, Pikuni, Siksika) tracked the movements of prairie wildlife and the rhythm of the seasons across the vast grassland landscape, but the arrival of industrialized European immigrants signalled the beginning of the greatest transformation of this grassland ecosystem since the glaciers.

The first European explorers travelled up the meandering rivers through the northwest Great Plains in the late-18th century. Because European settlement ensured title of these territories for the Dominion of Canada, the development of a trans-Canada railway through these newly acquired territories became a priority of the Dominion Government. Multiple disease epidemics, the loss of the indispensable Plains bison (*Bison bison bison*) food resource, and hostilities with government armies concluded the domination of the northern Great Plains by aboriginals (e.g. Cree and Blackfoot Confederacy (Blood, Peigan and Siksika)), and initiated the industrialisation of the Canadian prairie (Waldman 1999). To fund the railway construction, the Dominion Government transferred title of the vast rangelands gained from treaty negotiations to the Canadian Pacific Railway (CPR), and gave away or sold much of the remaining rangeland at bargain prices to immigrant farmers who agreed to settle and cultivate these remote grasslands.

The extension of the railway into the prairie region was the single greatest vector for ecosystem change, as it transported immigrant settlers west to the prairie, and their goods to the eastern markets. Indeed, the eradication of the bison (*Bison bison*) and most of the large prairie predators followed the progress of the railway through the northern grasslands.

The political expediency of settlement sometimes resulted in the cultivation of grasslands that had marginal value for crop production and many early farming attempts were devastated by droughts. The hostile climate and remoteness of the western prairie limited immigration and the rate of grassland cultivation until 1935 when the CPR turned over existing irrigation networks and ~500 000 ha of land to farmers to promote settlement (EID and Alberta 1995). Many displaced farmers settled these irrigated grasslands in Alberta from drought afflicted areas in Saskatchewan because of the promise of irrigation water for crop production.

Current Management Issues

The elected board of the Eastern Irrigation District (EID) manages the remaining

native rangelands for community cattle grazing, and has greatly increased the range of the irrigation networks (reservoirs and canals) to support both grazing and a diversity of mixed crops. In addition to agricultural uses, the EID manages these valuable water resources for industry, municipalities, recreation, tourism, and wildlife (EID and Alberta 1995).

Although the discovery of natural gas in Alberta occurred in 1883 during construction of the CPR, only in recent decades has the exploitation of abundant petroleum reservoirs, such as oil and natural gas, replaced agriculture as the major contributor to local economies and ensuing contemporary growth of cities and towns. The remarkable growth of the petrochemical industry has replaced agriculture as the primary contributor to the fragmentation of remaining native prairie expanses.

Projected reduced downstream river flow volumes resulting from the rapidly receding Rocky Mountain glaciers threaten to exacerbate current water shortages in the Canadian Prairie Provinces (e.g., Demuth and Pietroniro 2003). These long-term flow reductions jeopardize the future of existing irrigation crops, and should be carefully considered before more native grasslands are cultivated for drought intolerant crops (e.g., proposed cultivations for potato production). Furthermore, extensive native prairie losses could result from the proposed open-pit excavation of coal deposits for energy production as the existing liquid and gas petroleum reserves become depleted or uneconomical for production. Comparatively, grazing of native prairie could continue in perpetuity with proper grazing management and adequate precipitation.

Study Area Description

The study area (Figure 1-2) encompasses approximately 650 km^2 of prairie in the Dry Mixed-grass Ecoregion (Strong and Leggat 1992) in southeast Alberta, between the town of Brooks and the city of Medicine Hat. The study area is physically bounded on the north by the divided four-lane Trans-Canada Highway

(Hwy 1), to the west by irrigated croplands between the village of Tilley and the hamlet of Rolling Hills, and to the south by dry-land cultivation and the Bow River. The Newell County border politically partitions the open prairie along the eastern edge of the study area. The prairie plains are generally flat – the only apparent topographical relief is from small undulating hills in the southeast and western periphery of the study area and the valley of the 12-Mile Coulee Reservoir that spills into the Bow River in the southwest corner of the study area. Similar flat mixed-grass prairie continues for > 20 km east of the study area, but undulating grassland topography becomes more prominent north of Hwy 1.

Native prairie management involves adjusting stocking rates and grazing duration based on range condition, and moving large community-owned cattle herds between large grazing enclosures that are typically several square kilometres in area. Such large grazing partitions permit a diversity of grazing intensities; for example, very heavy grazing around water sources and salt blocks is contrasted by low grazing intensity in rangeland distant from these sites. This habitat complexity promotes wildlife biodiversity by providing distinctly different habitats for wildlife adapted to either heavy or light grazing intensities (e.g., Davis et al. 1999).

Brown Chernozemic soils are most common, while small undulating hills are typically stabilized sand dunes, glacial till or lacustrine deposits. Native grasses such as needle and thread (*Stipa comata*), June grass (*Koeleria macrantha*), blue grama (*Bouteloua gracilis*) and wheatgrasses (*Agropyron* spp.) dominate the gramnoids. Sagebrush (*Artemisia cana*) dominates the shrubs. In addition to grasses, moss phlox (*Pholx hoodii*) and lichens (*Cladina* spp.) are the predominant groundcover. When the prairie sod has been disturbed, native succulents, such as prickly pear (*Opuntia polyacantha*) and pincushion cacti (*Coryphantha vivipara*), and bare soil can become the greatest proportion of ground cover. Sandberg's bluegrass (*Poa sandbergii*), Nuttall's alkali grass (*Puccinellia nuttalliana*), gumweed (*Grindelia squarrosa*), and bulrushes (*Scirpus*

validus) are common in ephemeral alkali wetlands, while cattails (*Typha latifolia*) proliferate on permanent wetland-reservoirs. Trees grow on the surrounding farmsteads, the railway, and in the river valley, but are absent from the prairie uplands.

Non-native invasive gramnoids, such as crested wheatgrass (*Agropyron pectiniforme*), slender wheatgrass (*A. trachycaulum*), and Russian wild rye (*Elymus junceus*), have been introduced to provide early season forage for cattle (i.e., tame pasture). These grasses are also planted to stabilize bare soils in disturbed areas such as petroleum developments and ditches along gravel roads. Invasive weeds such as Russian thistle (*Salsola kali*) and koshia (*Kochia scoparia*) can proliferate in areas after native vegetation has been reduced or eliminated, and on bare soil. Currently < 10% of the rangeland in the study area has been ploughed and seeded with cultivars. Thousands of kilometres of gravel roads, trails, and pipelines that result from petroleum industry activities are increasingly linearly fragmenting remaining native prairie.

The climate of the study area is arid continental, characterized by long cold winters and short summers. Summer temperatures typically range from nocturnal lows of 8°C to diurnal highs of 23°C, and average 15°C May-August; however daily maximum temperatures commonly rise above 30°C in July and August (Strong and Leggat 1992). The greatest volume of precipitation typically falls in June, with May-August precipitation accounting for 54% of the annual volume of precipitation (Strong and Leggat 1992). Precipitation at the town of Brooks, 25 km NW of the study area, reveals that above average annual precipitation in 1999 (39.4 cm) was followed by drought conditions in 2000 (18.1 cm) when precipitation was approximately half the 1971 to 2000 average (34.8 cm; Environment Canada 2003). Summer and winter drought conditions severely limited the growth of vegetation in 2000, contributing to conditions favourable for wind erosion in many areas.

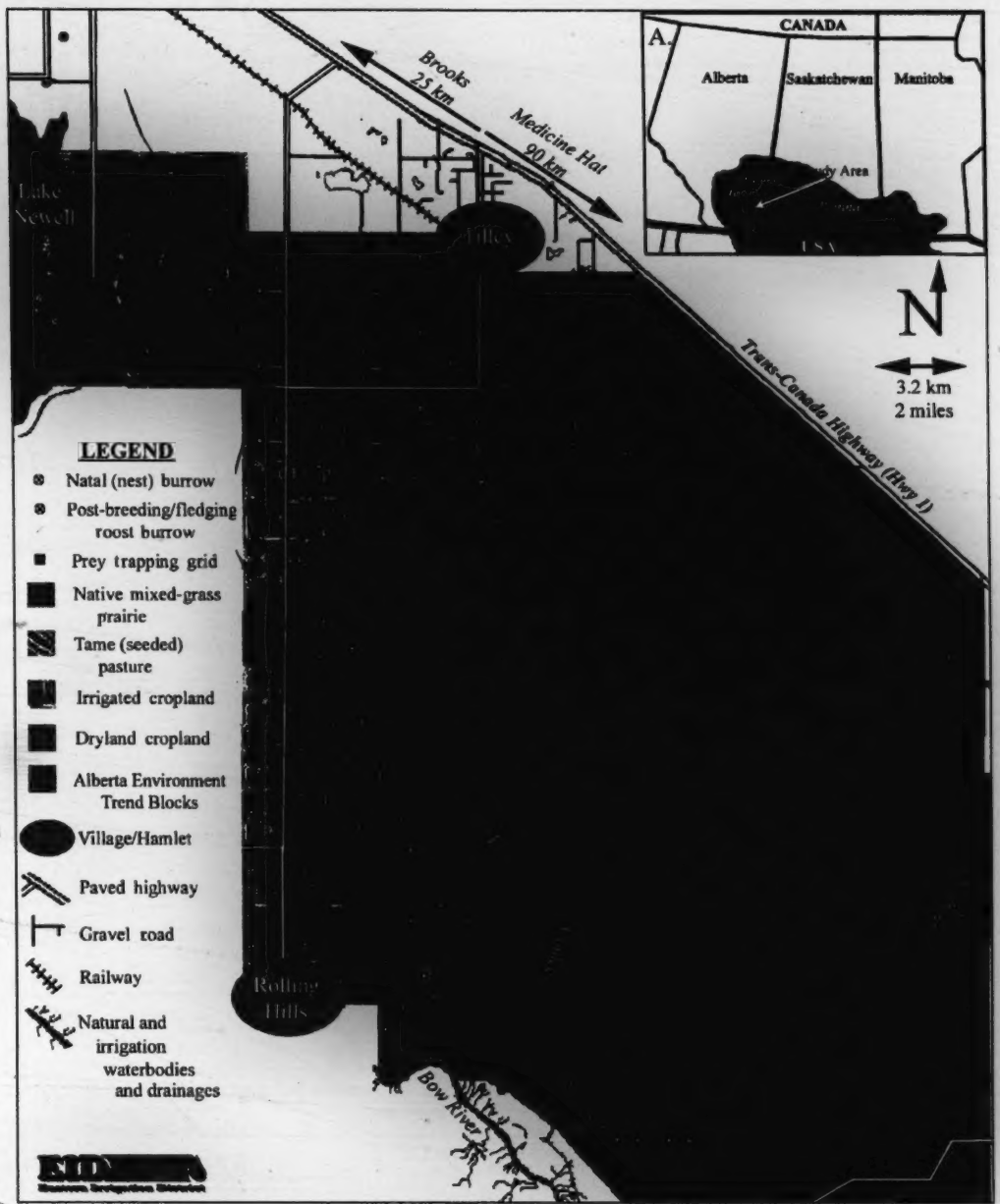

FIGURE 1-3. A composite air-photograph of the study area in southern Alberta illustrating the locations of nest and dispersal roost burrows, prey-trapping grids, principle habitat types, towns, AB Trend Blocks, and principle landscape features. Inset (A) illustrates the location of the study area and the historical (grey) and current (black) breeding range of Burrowing Owl in the three Canadian Prairie Provinces (range extents adapted from Haug et al. 1993).

CHAPTER 2

JUVENILE SURVIVAL FROM FLEDGING TO MIGRATION

INTRODUCTION

Understanding survival rates and sources of mortality in wildlife populations is invaluable for identifying particularly vulnerable cohorts or populations, and is important to our understanding of population dynamics. As well, quantifying comparative demographic information in different areas enables more accurate assessments of breeding habitat quality (Anders et al. 1997). Because large proportions of immature birds raised to independence do not survive to breed (Botkin and Miller 1974, Glue 1973, Hirons et al. 1979, Lack 1946, Newton 1979), it is important to evaluate the survival probabilities of immature birds in declining populations. Because of the propensity for reduced survival of immature birds to limit population growth, a fair amount of research has directed on quantifying juvenile survival in migratory Burrowing Owl populations in Canada, as strategized in the *National Recovery Plan for the Burrowing Owl* (Hjertaas et al. 1995).

First-year survival of immature Canadian Burrowing Owls is the product of the survival probabilities from four important stages of their life cycle: 1) the nestling period when adult care influences immature nestling survival, 2) the post-fledging period when juveniles become independent of parental provisioning, 3) the migratory period when juveniles can fly thousands of kilometres into the southern United States and Mexico, and 4) the winter period when the juveniles reside in southern habitats. Nestling survival (May-June) is dependent on parental investment, and can be limited by food shortages (Wellicome 2000). Parental provisioning terminates when nestlings fledge at six weeks of age (July-August), and the independent juveniles that survive the post-fledging dispersal period migrate south from northern breeding grounds by mid-October. Burrowing Owls can successfully breed after their first winter, thus evaluating survivorship and the

factors that affect survival in the first year of life may provide insight into whether recruitment is limiting population growth and recovery.

Physically marking birds (e.g., leg-bands) is a useful method of determining apparent survival when movements are restricted to areas such as nest sites and natal territories, but when movements are not locally constrained, the recovery or re-sighting of marked individuals underestimates actual survival rates because individuals that permanently emigrate out of search areas are assumed dead when they may yet be alive but undetected (Botkin and Miller 1974, Burnham et al. 1996, Pollock et al. 1990). The difficulty in recovering dispersing post-fledging juvenile Burrowing Owls confounds estimations of apparent survivorship (Clayton 1997, Gleason 1978, Millsap 2002, Thomsen 1973).

Tracking radio-tagged animals provides survival data that are superior to traditional capture-recapture or band-recovery methods because radio-tags: a) increase the range of monitoring, b) increase the accuracy of survival estimates, c) allow for more accurate determination of mortality causes by permitting re-location of an animal after it perishes, and d) allow for estimates of survival determined in specific stages of the life-cycle (Pollock et al. 1989, White and Garrot 1990).

In the late summers of 1999 and 2000, in relatively contiguous native mixed-grass prairie, I tracked radio-tagged juvenile owls until migration to quantify post-fledging survival probabilities (i.e., rates) and causes of mortality in a population with an uncharacteristically stable population trend over the past decade (Shyry et al. 2001). Principally, I contrast juvenile survivorship in this population near Brooks, with three other studies (see Table 2-4): 1) concurrent research ~500 km east in highly fragmented habitat of the Regina Plain (Todd et al. 2003), 2) a prior study in both the fragmented Regina Plain and in similarly contiguous prairie ~150 km north near Hanna (Clayton and Schmutz 1999), and 3) peripherally to previous research in southwest Idaho (King 1996). I review juvenile survivorship

in relation to apparent population trends, level of native habitat retention, and conservation management of the species. I discuss the disparity in juvenile survivorship between the more stable populations and the terminally decreasing populations, and between populations inhabiting landscapes with opposite proportions of native prairie retention.

METHODS

Tagging and Tracking

Owls and nests were located using road-side searches in 1999 and 2000 (Sissons 2003), but the search protocol in 2001 involved an 800 m grid point-count call-playback (Haug and Didiuk 1993) survey encompassing all native rangeland, except Alberta Environment Trend Blocks (see Figure 1-3) within the study area. Trend Blocks were surveyed for owls in July 1999-2001, and band status of adult owls was assessed at that time (R. Russell pers. comm.). Small patches of rangeland interspersed within the irrigated croplands adjacent to the study area were not searched.

To ensure members of the brood were a sufficient size for a tag (mass > 120 g) and to try to capture nestlings prior to fledging and dispersal away from natal territories, trapping commenced when plumage indicated at least one nestling was older than 32 d (Priest 1997), and at least one juvenile was observed competently flying short distances (> 50 m) in the natal territory. Evening trapping corresponded with a higher frequency of juvenile activity (Best 1969), other reported trapping successes (Martin 1971), and suggested trapping times (Plumpton and Lutz 1992). Nestlings were captured using one-way door traps (see Banuelos 1997 and Winchell 1999 for similar trap designs) in burrows entrances, and in bow-nets baited with live and dead mice adjacent to burrows. Traps were continuously monitored from 200-500 m away. All captured owls were fitted with an aluminium numbered leg band (USFWS band) and a colour coded alphanumeric leg band (Acraft Sign and Nameplate Co., Edmonton, AB) for individual identification. Radio-tags (Holohil Systems, Newmarket, ON)

weighing ≤ 5% of body mass (Caccamise and Hedin 1985, Ornithological Council 1997) were fastened on two randomly selected nestlings from broods with ≥ 3 individuals, or on a single nestling when only one individual was captured or produced. After successful trapping sessions, one house mouse (*Mus musculus*) was given to broods ≤ 3, or two mice were left at nests with > 3 nestlings, in an effort to compensate for any potential reduction in prey deliveries during trapping.

Long burrow tunnels restricted access to subterranean nests, precluding accurate determination of hatching dates, so I estimated the age of captured nestlings by comparing feather lengths to growth curves (T. Wellicome unpublished data). These growth curves illustrate that the central tail feather and ninth primary feather growth curves are robust for aging until 50 d and 45 d respectively, after which the curves become asymptotic. Because prolonged precipitation can cause food related stress that can delay growth rates (King 1996, Wellicome 2000), feather lengths from 1999 and 2000 were compared to growth curves from breeding seasons with similar volumes of precipitation (1992 and 1996 respectively). I assume that the volumes of precipitation in 1992 and 1996 are relative to the potentially delayed growth rates in 1999 and 2000.

Tagged juveniles were tracked while they nocturnally foraged in 1999, and while diurnally roosting and nocturnally foraging in 2000. I attempted to locate and determine the survival status of tagged juveniles ≤ 3 d from the time the tag was attached until the owl died or dispersed out of the study area, but inclement weather and wide-ranging dispersals confounded this schedule. Radio signals were detected using portable receivers (Lotek SRX 400, Carp, ON, and a Wildlife Materials Inc. TRX 1000S, Carbondale, IL), and an omni-directional antenna mounted on the roof of field vehicles or a hand-held three-element antenna.

Foraging owls were typically located remotely, although they were occasionally flushed by field trucks when foraging on or near roads. Diurnally roosting owls were generally flushed every 10 d during pellet collections. Because the range of

the tags was < 1 km from the ground, but up to 8 km from the aircraft, 2-3 aerial tracking excursions between late August and early October each year attempted to ensure that all mortalities were detected within the search perimeter. Aerial tracking followed a 10 km grid pattern, to a radius of 30 km outside the study area in 1999, and to a 50 km radius in 2000, but these flights were truncated northeast of the study area because of flight restrictions over Canadian Forces Base (CFB) Suffield.

Mortality and Censoring

The remains of dead owls were carefully scrutinized to determine the cause of death (Einarsen 1956). The causes were categorised as: 1) *predation* – avian predators indicated by plucked feathers, usually in the same location as the tag or at a plucking roost; mammalian predators indicated by a chewed carcass, feathers, bones and/or tag, and by recent badger observations or excavations at occupied burrows; 2) *anthropogenic* – indicated when the carcass was found on or near the road with apparent trauma from a vehicle collision or snagged on barb-wire fencing, 3) *unknown* – no apparent evidence of trauma or other obvious source of mortality (e.g., starvation, disease), and 4) *tag failure* – the owl was observed with a damaged tag (e.g., antenna removed), and the range of the tag was eliminated or impractically reduced (< 50 m).

The date of mortality was assumed to be the day following the last live observation for mortalities found ≤ 2 d (77%). For those instances when the mortality was found 3-4 d (18%) after the last live observation, the date was estimated using the 40% rule (Miller and Johnson 1978). In the sole instance (6%) when 6 d had passed before the dead owl was found, the mortality was assumed to have happened on the sixth day because the carcass was neither scavenged nor decomposed. The location of dead owls was determined using a hand-held Global Positioning System (GPS) that provided < 30 m error in 1999 and < 10 m error in 2000. When a tagged owl could no longer be located during ground or aircraft searches, it was assumed to have permanently (e)migrated from

the study area and the censoring date was entered in the survival model as the day following the final live observation.

Predator Abundances

The relative abundance (individuals per km) of diurnal raptors was estimated in June-July of both years by identifying and enumerating raptors while driving 20 kph along a 40 km route of gravel roads that bisect the study area NW to SE. Raptor surveys were constrained by the following parameters: 10:00 - 14:00, wind speed < 20 kph, cloud cover < 50%, temperature > 15°C, and no prolonged showers or rain.

Infrequently observed carnivores of the open prairie habitat include badgers, coyotes, and small weasels (*Mustela* spp.). Closer to the farmlands west of the study area, red foxes, striped skunks (*Mephitis mephitis*), and a recent colonist, the raccoon, were more commonly observed. Extensive control of coyotes likely contributes to their reduced abundance in the district, but the other mammalian predators are less frequently persecuted on the remote prairie uplands than they were historically. I did not quantify mammalian predator abundances because of the large effort and time required to quantify a diversity of low density animals in this expansive study area.

Data Analyses

To calculate cumulative juvenile survival probabilities, I started survival analyses 41 d post-hatch when juveniles fledge (Wellicome 2000) and concluded analyses on the date of the last live observation in or near the study area. To eliminate potential biases introduced by non-independence of sibling survival probabilities (e.g., Massot et al. 1994), one randomly selected tagged juvenile from each nest was included in the juvenile survival analyses (Todd et al. 2003). Sibling pairs were included in an analysis assessing the influence of tag style on survivorship (Chapter 4). Because of indistinguishable plumage, I was unable to separate

juveniles by sex, but there is no evidence of sexually-biased juvenile survival (Todd et al. 2003).

Because food-limited mortality is a principal cause of Burrowing Owl brood reductions (Wellicome 2000) and the heaviest siblings in broods tend to have higher survival (Thomsen 1971, Todd et al. 2003), I assessed the impact of food shortage on juvenile survivorship by including mass at time of capture as a covariate in survival analyses. Because earlier hatched nestlings from asynchronously hatched broods are greater mass than younger siblings, I also included fledge date (age) and a relative measure of body condition (mass (g)/wingspan^3 (mm) X 100; Sodhi et al. 1991) as covariates in survival analyses.

Kolmogrov-Smirnov tests assessed data normality: *t*-tests were applied to normal data, while Mann-Whitney U tests compared non-parametric medians and Spearman's Rank tests were used to find the correlation of non-parametric variables. The Kaplan-Meier (KM) procedure produced cumulative survival probabilities ($\hat{s}$) and graphs (Kaplan and Meier 1958, Pollock et al. 1989), while log-rank tests (Efron 1977, Tsai et al. 1999) tested the equality of survival probabilities and Cox regression (Cox and Oakes 1984) assessed the influence of covariates on survival. The KM method calculates the cumulative survival function of an arbitrary animal or cohort at observed events (i.e., death or censored) from the beginning of the study (i.e., fledging) and allows for entry of censored observations when the tagged animal disappears (e.g., movements out of study area, tag failures, etc.). The KM method assumed that: 1) the animals have been randomly selected from both sex and age groups, 2) radio-tags do not affect the fate of the animal, 3) individual survival times are independent, 4) probability of not relocating the animal is random, and 5) the survival function is constant for previous and newly tagged animals. All analyses were conducted using SPSS software (SPSS 1999) and unless otherwise stated, results are presented as mean ± SE. Because of small sample sizes, statistical significance was assessed at $\alpha = 0.10$.

RESULTS

In 1999 and 2000, I captured and banded 106 nestlings (63 and 43 respectively) and from these I placed 51 radio-tags (29 and 22 respectively) on randomly selected nestlings prior to fledging. One nestling was omitted from survival analyses because the tag failed < 1 d after attachment, and one underweight (i.e., outlier) but untagged juvenile was excluded from morphological comparisons. The median fledging dates were 14-July-1999, and 13-July-2000. Post-hoc t-tests indicate that although there were no annual morphological differences between nestlings (Table 2-1.A), randomly tagged nestlings were older and heavier than untagged nestlings (Table 2-1.B). Tagged juveniles that died in the study area tended to be those that had less mass at capture than those that ultimately migrated (Table 2-1.C). Tagged juveniles were tracked for a total of 1593 post-fledging radio-days (31.9 ± 2.98) until the latest observation of a tagged juvenile in the vicinity of the study area 29-Sept-1999 and 02-Oct-2000.

Cumulative Juvenile Survival Probabilities

During the two annual post-fledging periods, 34% of all tagged juveniles died in the study area prior to migration. The greatest decrease in juvenile survival occurred in the first month of independence, and the average age at death was 56.1 ± 2.7 d (n = 17). Dead juveniles were found < 3 km from their nests (680 ± 226 m), and 35% of these were located in natal areas (delineated by the distance from the nest burrow to the furthest adult male natal roost). Age at death and the distance from the natal burrow were positively correlated ($r_s = 0.648$, $p = 0.002$), and there was an apparent trend for the risk of mortality to shift from badgers and accidents to avian predators as juveniles aged and dispersed away from natal territories.

After randomly selecting one tagged individual from each nest, 17 (1999) and 11 (2000) tagged juveniles were included in the KM survival model to produce cumulative survival probability functions (Figure 2-1). Although juvenile survival probability was lower in 1999 (0.606 ± 0.126) than 2000 (0.682 ± 0.154),

this difference was not significant (log rank = 0.96, $p = 0.328$), and both years were pooled to produce an aggregate survival function for this population (0.615 ± 0.106).

TABLE 2-1. Average nestling age, mass, and body condition at the time of capture, and results of post-hoc *t*-tests comparing these variables between nestlings captured in 1999 and 2000 (A), between tagged and untagged nestlings (B), and between tagged nestlings that eventually died in the study area and those that migrated (C) in southern Alberta.

A.	Nestling Variable	1999 (n = 62)	2000 (n = 43)	*t*	*p*
	Age (days)	36.89 ± 0.82	36.55 ± 0.76	0.29	0.773
	Mass (g)	131.32 ± 1.84	127.49 ± 2.57	1.25	0.216
	Body Condition (x 10^{-4})	37.94 ± 0.92	35.92 ± 7.50	1.37	0.173
B.	**Nestling Variable**	**Untagged (n = 54)**	**Tagged (n = 51)**	***t***	***p***
	Age (days)	35.46 ± 0.80	38.12 ± 0.80	2.36	0.020
	Mass (g)	124.01 ± 2.29	135.88 ± 1.57	4.22	<0.001
	Body Condition (x 10^{-4})	37.76 ± 1.09	36.46 ± 6.84	-0.89	0.376
C.	**Nestling Variable**	**Migrate (n = 33)**	**Death (n = 17)**	***t***	***p***
	Age (days)	37.85 ± 4.91	37.94 ± 6.62	0.06	0.956
	Mass (g)	137.95 ± 2.05	132.44 ± 2.30	-1.67	0.101
	Body Condition (x 10^{-4})	37.07 ± 6.12	36.09 ± 7.65	-0.49	0.625

Sources of Mortality

Predators were the principal cause of juvenile mortality in both years, causing 59% of juvenile deaths over the two breeding seasons (Table 2-2). Avian predators caused more than twice as many deaths as badgers, and on two occasions Northern Harriers (*Circus cyaneus*) were observed at fresh carcasses (H. Trefry pers. comm.). I was unable to detect an apparent relationship between raptor abundance and survivorship because juvenile survival and raptor relative abundance were both greater in 2000.

Vehicle collisions were the other apparent cause of juvenile mortality, but these accidents occurred only in 1999. In addition to the two tagged juveniles that died from vehicle collisions, six dead, untagged juveniles were located incidentally on remote gravel roads in 1999. In contrast, no tagged or incidental juvenile vehicle casualties were found in 1998, 2000, or 2001. Although one juvenile died after

becoming entangled by both its wing and the radio-tag antenna on a barbed-wire fence, an untagged juvenile similarly perished, suggesting that this type of accident occurs regardless of the tag.

I was unable to determine the cause of death for four juveniles because their intact remains did not show obvious evidence of predator activity or trauma. Although starvation has been implicated as a cause of death for juveniles (Todd et al. 2003), two of these unknown mortalities were the heaviest members of their brood at the time of capture, suggesting a cause of death other than starvation. These carcasses had deteriorated too much to accurately assess weight at the time of death.

Only necklace style tags failed (4 failures, 1 removed), and all but one tag failure occurred in 1999. Three owls were seen with damaged or absent antennae prior to dispersing from natal areas. The higher rate of tag-failures in 1999 typically resulted from owls damaging or removing necklace tag antennae. The frequency of tag-failure was reduced in 2000 by strengthening the antennae connections to the tag body with a protective sheath of plastic shrink tubing.

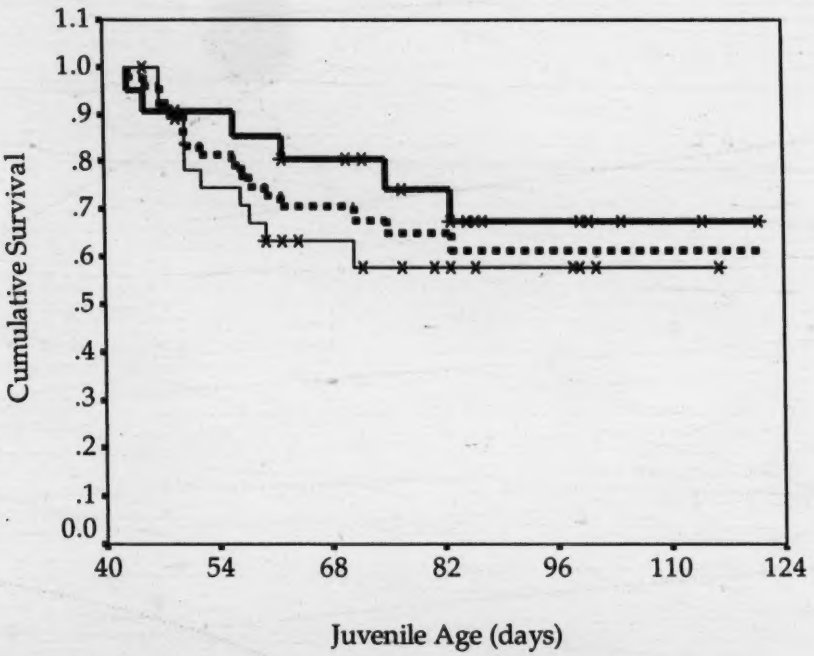

FIGURE 2-1. Cumulative survival probability of tagged juvenile owl in 1999 (thin line), 2000 (thick line), and 1999-2000 pooled (dotted line) in southern Alberta. Steps down indicate mortalities; splice markers (*) indicate censored events.

Band Returns

Band recoveries have been used to estimate apparent survival rates of birds, but re-sighting probability is typically dependent on fidelity to breeding territories. Extremely low first year return rates and recent migration research (Duxbury 2004) suggest that juvenile Burrowing Owls do not have high fidelity to natal territories. Therefore, the very few owls banded as nestlings which returned to the study area in subsequent years (Table 2-3) reflect natal fidelity and re-sighting probability rather than providing an index of annual apparent survival. The annual cohort with the highest annual rate of return was from 1998; in contrast none of the banded nestlings from the 2000 cohort were observed in subsequent years. All first-year returning owls successfully paired, and 80% of these pairs produced at least one owlet creating a successful nest. I was able to determine the sex of returning owls using behavioural clues during nesting: 71% were male

(three males and two females returned in their first year, one male was observed as a 2 yr old, and another male was observed when it was 3 yrs old).

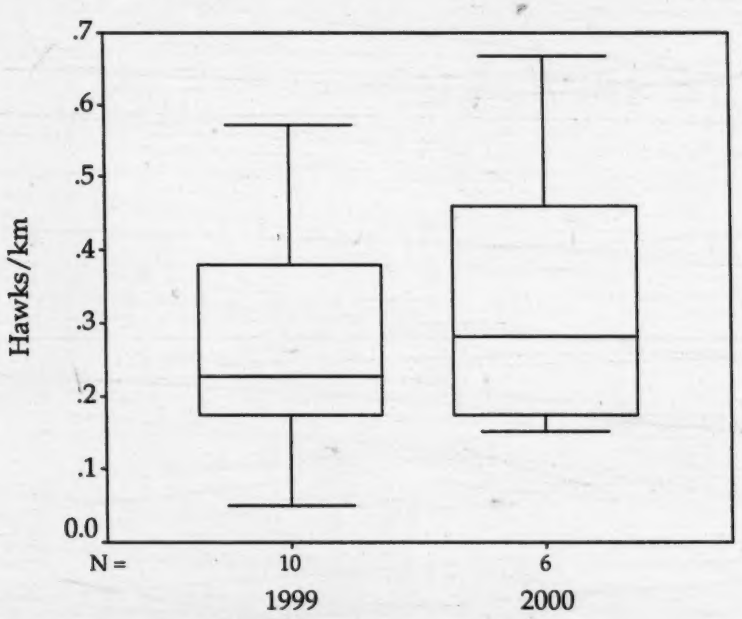

FIGURE 2-2. Relative abundance of large hawks observed during roadside surveys in 1999 and 2000 in southern Alberta.

Predator Abundances

The relative abundance (individuals per km) of large raptors capable of killing a Burrowing Owl, was greater in 2000 (Figure 2-3), principally resulting from an increase in Prairie Falcon sightings, but the difference was not significant (0.299 ± 0.045, $U = 26$, $p = 0.713$). When both years were pooled, the rank order became: Northern Harrier (5.94 ± 1.05) > Swainson's Hawk (2.94 ± 0.67) > Ferruginous Hawk (*Buteo regalis*; 1.87 ± 0.44) > Prairie Falcon (*Falco mexicanus*; 0.94 ± 0.46) > Red-tailed Hawk (*Buteo jamaicensis*; 0.13 ± 0.09). Because the Merlin (*Falco columbarius;* 0.69 ± 0.15) and the American Kestrel (*Falco sparverius*; 0.13 ± 0.09) are similar in body size to Burrowing Owls, they are unlikely predators of adults or fledged owls. Other large raptors infrequently observed during the summer in the study area but not observed during roadside

surveys include the Great Horned Owl (*Bubo virginianus*), Long-eared Owl (*Asio otus*), Short-eared Owl (*Asio flammeus*), and Golden Eagle (*Aquila chrysaetos*).

DISCUSSION

This study is the third to quantify post-fledging juvenile survivorship in the northern limit of the breeding range of Burrowing Owls in North America (Clayton 1997, Todd 2001), and the second to assess survivorship in relatively contiguous native rangelands. It is the first to assess survivorship in a population with a comparatively stable trend. These three variables provide the basis for discussion of the potential influence of disparate juvenile survival rates on population trend and the potential influence of habitat fragmentation on juvenile survivorship.

Juvenile Survivorship in Relation to Local Population Trend

If reduced juvenile survival is limiting population growth in the Canadian populations, survival rates should be positively correlated with the population trend. Excluding the summer of 1997, when superfluous prey resulting from an peaking vole population contributed to the survival until migration of all tagged juveniles by eliminating the effects of starvation and likely satiating predators (Todd et al. 2003), and ignoring the potential differences between methods to calculate survival probabilities (Table 2-4), juvenile survival is apparently higher in the Brooks population than in the terminally decreasing populations near Hanna (Clayton 1997) and Regina (Todd 2001). King (1996) provided the only other stage-specific estimate of juvenile survival in a locally abundant population in southern Idaho, and found a substantially greater proportion of post-fledging juveniles surviving to migration (85.6%) than reported for the Canadian populations (< 60%).

Lower survival rates in the two terminally decreasing populations (Regina Plain and Hanna) relative to the more stable populations (Brooks and Idaho), and a positive correlation between post-fledging survival and population size the

following year (Todd et al. 2003), both support the theory that juvenile survival is limiting population growth in the failing Canadian populations. The incorporation of these juvenile survival rates with additional demographic data (e.g., fledgling production, fidelity rates, prey abundance, etc.) into a population model would help explain the relative impact of reduced juvenile survival in the failing populations.

Juvenile Survival in Relation to Habitat Fragmentation

Immigration can be necessary for population persistence in poor-quality habitats if conditions are inadequate to maximize productivity, survival, and recruitment (see Pulliam 1998 for a discussion of *sink* habitats). Because the widespread destruction of the Canadian prairie has contributed to the invasion of novel predators, and may be a factor contributing to reduced prey abundances and frequency of prey population irruptions (Poulin 2003), it seems apparent that the loss and fragmentation of native prairie has reduced the quality of this habitat for Burrowing Owls. If native prairie loss affects survivorship, disparity in juvenile survival rates and sources of mortality should be evident in areas with differing levels of prairie habitat retention.

Effect of Fledgling Covariates – In the Regina Plain, supplementally provisioning lab mice as extra food to broods increased nestling survival (Wellicome 2000), and similarly no tagged juveniles died during a post-fledging period that coincided with a natural meadow vole (*Microtus pennsylvanicus*) population irruption (Todd et al. 2003). While I did not find a relationship between juvenile survival probability and hatch date or body condition, I found a trend for heavier fledglings to be more likely to survive until migration than those that were lighter. This trend concurs with Todd et al. (2003), who found that juveniles which survived to migrate were 6% heavier prior to fledging than those that perished. It appears that limited food availability detrimentally affects survival of immature owls, which could potentially limit population growth.

TABLE 2-2. Proportional cause-specific fate of all tagged juveniles (*n*) between fledging and migration 1999 – 2000 in southern Alberta.

Year	Survive	Predators		Anthropogenic		Unknown	Failed Tag
		Raptor	*Badger*	*Vehicle*	*Fence*		
1999 (29)	0.483 (14)	0.103 (3)	0.069 (2)	0.069 (2)	0.034 (1)	0.103 (3)	0.138 (4)
2000 (22)	0.682 (15)	0.182 (4)	0.045 (1)	0.000 (0)	0.000 (0)	0.045 (1)	0.045 (1)
Pooled (51)	0.569 (29)	0.137 (7)	0.059 (3)	0.039 (2)	0.020 (1)	0.078 (4)	0.098 (5)

TABLE 2-3. The percent (n) of nestlings banded 1998 – 2000, returning to the study area 1999 – 2001, and the first year, overall annual cohort, and cumulative total return frequencies in southern Alberta

Year Banded	Mortalities	Year of Resighting			First Year	Cohort
		1999	2000	2001		
1998 (16)[a]	-	6.3 (1)	0 (0)	6.3 (1)	6.3 (1)	12.5 (2)
1999 (63)	17.5 (11)	-	6.3 (4)	1.6 (1)	1.6 (4)	9.6 (5)
2000 (43)	16.3 (7)[b]	-	-	0 (0)	0 (0)	0 (0)
Total (122)	14.8 (18)	6.3 (1)	7.4 (5)	6.7 (7)	-	-

[a]Data kindly provided by R. Sissons.

[b]One incidentally found untagged mortality included.

TABLE 2-4. Post-fledging juvenile survival probabilities in Canadian populations with disparate population trends and in landscapes with reverse levels of native prairie habitat retention. Survival data from 1997 in the Regina Plain is not pooled with the other years (1998-2000) because of the obvious disparity with other documented rates of survival.

Study Area	Population Trend	% Native Prairie	Predominant Land Use	Research Years	Survival Metric	Total Tags
Hanna, AB	Terminal	>80	Grazing>Cereal Crops>Petroleum	1995-1996	0.45[a]	21
Regina Plain, SK	Terminal	<10	Cereal Crops	1996	0.48[a]	25
Regina Plain, SK	Terminal	<10	Cereal Crops	1997	1.00[b]	12
Regina Plain, SK	Terminal	<10	Cereal Crops	1998-2000	0.55[b]	52
Brooks, AB	Comparatively Stable	>90	Grazing>Mixed Crops>Petroleum	1999-2000	0.62[b]	28

[a]MICROMORT (Mayfield) daily survival analysis.

[b]Kaplan-Meier survival analysis.

Anthropogenic Impacts – In more expansive prairie habitats, anthropogenic factors were related to 6% of juvenile fatalities in this study (Table 2-2), and 0% in Hanna (Clayton and Schumtz 1999), somewhat lower than 9% reported by Todd et al. (2003), and substantially lower than 53% reported by King (1996) in Idaho. Deaths related to human activities in Canada were caused primarily by collisions with vehicles, and secondarily by entanglement on barbed-wire fencing. In contrast, gunshot killed the most juveniles in Idaho, followed by traffic collisions, entanglement on barbed-wire fencing, and finally by drowning (King 1996). Burrowing Owls across the continent are apparently susceptible to traffic collisions because vehicular deaths are reported across their breeding range: Alberta (Clayton and Schumtz 1999), California (Thomsen 1971), Idaho (Gleason 1978, King 1996), Florida (Millsap 2002), North Dakota (Konrad and Gilmer 1984), Oklahoma (Butts 1973), and Saskatchewan (Haug and Oliphant 1990, Clayton and Schmutz 1999, Todd et al. 2003). In the fragmented Regina Plain, vehicle collisions killed 6% (Todd et al. 2003) and 17% (Clayton and Schmutz 1999) of post-fledging juveniles, whereas in more contiguous prairie vehicle collisions have killed between 0% (Clayton and Schmutz 1999) and 4% (Table 2-2) of juvenile owls, suggesting a negative correlation between traffic rates and juvenile survival.

In this study area, nocturnal traffic is generally absent because the prairie is not developed for settlement; the only buildings are uninhabited petroleum industry installations (e.g., battery, compressor, and meter stations). Fatal vehicle collisions occurred on roads nearest nests during the initial stages of fledging (July to mid August), and in 1999 coincided with a spike in the frequency of nocturnal traffic related to a multi-rig 24 hr drilling program in the area. In contrast, no owls were found dead on the study area roads in 1998, 2000 or 2001. Juvenile owls were frequently observed foraging along roads and ditches at night once they were able to fly (see Chapter 5), a foraging behaviour also observed in adults (Haug and Oliphant 1990, Scott 1940). But unlike adult males, juveniles did not consistently flush when a vehicle approached, even when the vehicle travels at low velocity (< 20 kph). Millsap (2002) also found most road mortalities on residential streets with reduced speed limits (≤ 56 kph) in Florida. The juvenile traffic fatalities in these remote rangelands introduced an anthropogenic mortality factor more common to settled landscapes and contributed to reducing the 1999 juvenile survival rate closer to rates observed in the more developed Regina Plain.

A congener of the Burrowing Owl, the Little Owl, also nocturnally forages on right-of-ways and roads, and road casualty is the first cause of non-natural death of this owl in Europe (Fajardo et al. 1998). Furthermore, more Little Owls die when the habitat adjacent to the road provides greater foraging opportunities whereas fatal collisions are reduced on roads with a higher availability of perching sites and during higher traffic frequency (Hernandez 1988). In this study, six of the eight locations where juvenile owls died from a collision with a vehicle have a barbed-wire fence along the roadside ditch, so perches along roads do not appear to reduce juvenile road mortality in a manner similar to Little Owls.

Habitat type and configuration adjacent to roads can contribute to higher prey abundances than observed on upland native prairie (see Chapter 5), and prey visibility is not obscured by vegetation on bare roads. Roads with crepuscular and

nocturnal traffic can act as ecological traps for inexperienced juvenile owls attracted to these sites by increased prey abundance and availability resulting from habitat alterations associated with road construction. Road-signs that request drivers slow down near Burrowing Owl nests (Skeel et al. 2001) may educate and create public awareness, but may not achieve the objective of reducing traffic fatalities unless they also successfully dissuade crepuscular and nocturnal travel on roads near nests in July and August during fledging. The consistently increasing road density across the Great Plains may contribute to more owls being injured and killed by vehicles, and greater scrutiny of the necessity of these linear fragmentation corridors is warranted for Burrowing Owl conservation.

Effect of Predators – A greater proportion of juveniles were killed by raptors in 2000, a year with higher large raptor abundance. Northern Harriers (Table 2-2) and Swainson's Hawks were observed killing owls, and these raptors are also implicated in juvenile fatalities in Hanna and the Regina Plain (Clayton and Schmutz 1999, Todd 2001). Although Ferruginous Hawk's commonly nested on platforms erected throughout the study area as a conservation measure for this threatened species (Schmutz et al. 1984), there was no evidence that these hawks preyed upon any juvenile owls. Roadside surveys suggested that Northern Harriers were the most abundant avian predator in the study area rangelands and this dominance may be related to the creation and maintenance of wetland-reservoirs attracting nesting Harriers. Because the remains of juveniles and their tags were located at the entrance and inside nest burrows, badgers were the only mammalian predator implicated in the death of juvenile owls.

In more expansive prairie habitats, predators were the primary source of juvenile mortality, killing 18% of juveniles in this study (Table 2-2), and 55% of juveniles in Hanna (Clayton and Schmutz 1999). Raptors killed twice as many juveniles as mammalian predators (Table 2-2), and although the trend was similar, the difference was not as great in Hanna (Clayton and Schmutz 1999). In the more

fragmented habitat of the Regina Plain, Clayton and Schmutz (1999) attributed an equal proportion of deaths to predators (18%) and anthropogenic causes (17%), while mammals (10%) killed slightly more juveniles than raptors (8%). In contrast, Todd et al. (2003) found that raptors (24%) killed the most juveniles, and that human disturbance (9%) and starvation (8%) caused an equal proportion of deaths. While Todd et al. (2003) showed that deaths related to anthropogenic factors increased seasonally in a predominantly agricultural landscape, in more contiguous prairie, I found that only raptor mortalities continued as juveniles dispersed from natal territories.

CONCLUSION

I found relatively higher post-fledging juvenile survival rates in a Burrowing Owl population residing in expansive but linearly fragmented prairie habitat near Brooks, than had been found in other Canadian populations residing in the more cultivated landscape of the Regina Plain (Clayton 1997, Todd 2001). Similarly, Todd et al. (2003) noted a trend for higher juvenile survival in larger (> 64 ha) versus smaller prairie patches. In contrast, Clayton and Schmutz (1997) reported no difference in overall survival rates between the Regina Plain and more contiguous prairie near Hanna, which had a level of fragmentation similar to the Brooks area; however, they found a higher risk from anthropogenic deaths in the more fragmented prairie of the Regina Plain.

Apparently reduced juvenile survival in more fragmented landscapes may be indicative of negative impacts of habitat fragmentation on Burrowing Owl demography. Further analyses that incorporate these survival data into a demographic model (T. Wellicome pers. comm.) will evaluate whether the rates of juvenile survival observed in Canadian populations are limiting population growth.

CHAPTER 3

EFFECT OF RADIO-TAG STYLE ON JUVENILE SURVIVAL

INTRODUCTION

Radio-tags facilitate our understanding of wildlife behaviour and demography, and with prudent application may not incur excessive costs to the study animal, but radio-tags have adversely influenced survivorship, reproduction, and behaviour in some animals (see Calvo and Furness 1992 for a review). Assuring tagged individuals remain unaffected by the tag is requisite for unbiased analysis of survivorship, but the potentially negative effects of radio-tags on Burrowing Owls are infrequently evaluated.

Radio-tags of various sizes and configurations (i.e., harness assembly) have been attached to Burrowing Owls to investigate foraging habitat selection (Haug 1985, Sissons 2003), dispersal behaviours (Clayton and Schmutz 1999, King and Belthoff 2001, Todd 2001), time budgets (Plumpton 1992), survivorship (Clayton and Schumtz 1999, King 1996, Todd 2001), and tag effects (Conway and Garcia 2005, Gervais et al. *in press*). Five studies have found contradictory impacts after scrutinized potential tag effects on Burrowing Owls: 1) Plumpton (1992) found that tagged adults spent less time resting and alert, more time away from burrows, and can have reduced productivity compared to untagged owls, 2) Clayton (1997) found similar survivorship between tagged and control nestlings, 3) Todd et al. (2003) found no difference in survival between post-fledging juveniles wearing a necklace or a backpack style tags, 4) Conway and Garcia (2005) did not find a negative effect of radio-tags on the probability of natal recruitment, and 5) Gervais et al. (*in press*) found owls carrying radio-tags to return at rates half that of control owls marked with leg-bands.

I compared sibling owls wearing similarly sized tags attached with differently configured harnesses to evaluate potential effects of radio-tags on post-fledging

juvenile survivorship. I present evidence that necklace style tags may negatively influence juvenile owl survival relative to backpack style tags.

METHODS

Juveniles were captured and tagged in natal territories in the week immediately prior to fledging at 42 d. A necklace and a backpack style radio-tag (Holohil Systems Ltd., ON, CAN), weighing ≤ 5% of body mass (Caccamise and Hedin 1985, Ornithological Council 1997), were individually fastened on two randomly chosen siblings from 15 broods with ≥ 3 nestlings. Nests with only a single nestling tagged were excluded from this analysis. The tags were permanently fastened to owls to facilitate overwintering investigations (G.L. Holroyd unpubl. data), but tagged owls that returned to the study area after migration were recaptured so that the tag could be removed, and the owl was inspected for any apparent damage caused by the tag (e.g., bruising, chafing, feather loss, etc.).

Necklace collars were constructed of soft plastic tubing covering an elasticized cord, with the body of the tag hanging ventrally and the antenna erected vertically from the dorsal side of the owls neck (Figure 3-1). The plastic tubing reduced the propensity for skin abrasions from the elastic cord, and protected the cord from owl-caused damage. The elastic cord stretched over the head of the owl during attachment, and contracted afterwards allowing a 1 cm gap between the collar and the neck of the owl to ensure sufficient space for prey ingestion and pellet regurgitation. This necessary gap also caused the body of the tag to dangle freely, particularly when the owl was in flight.

Backpack straps were fashioned from non-abrasive Teflon ribbon (Bally Ribbon Mills, Bally, PA, USA) that crossed across the breast of the owl, and fastened to the top and bottom of the tag in the centre of the owls back. Owls wearing backpack tags would preen the body of the tag and the harness under their body feathers until the vertically projecting antenna was the only part of the tag visible. Again, a 1 cm gap was left between the backpack harness and body of the owl to

permit body growth, but relative to necklace tags, the tag was securely fastened to the owl.

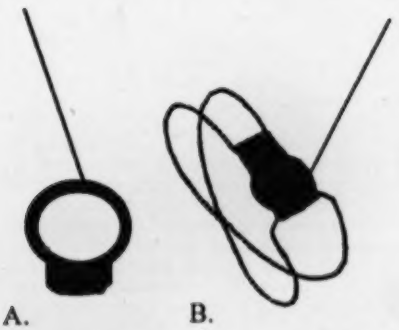

FIGURE 3-1. Configuration of the necklace (A) and backpack (B) style radio-tags placed on two sibling owls.

All analyses were conducted using SPSS software (SPSS 1999) and unless otherwise stated results are presented as mean ± SE. Statistical significance was assessed at $\alpha = 0.10$.

RESULTS

Five sibling pairs in 1999, and 10 sibling pairs in 2000, were given one backpack and one necklace style tag for a total of 30 tagged juveniles. Because nestling age, mass, and body condition at the time of capture were not different between 1999 and 2000 (Table 3-1.A), both years were pooled. There was no difference in age, mass, or body condition between siblings pooled by tag style (Table 3-1.B). Only three (20%) juveniles with backpack tags died prior to migration, compared to eight (53.3%) with necklace style tags. The cumulative survival probability (Figure 3-2) of the cohort fitted with backpacks ($\hat{s}_{15} = 0.758 \pm 0.127$) was significantly greater (log rank = 3.57, $p = 0.059$) than the cohort wearing necklace tags ($\hat{s}_{15} = 0.457 \pm 0.131$). Raptors were the primary cause of death for owls with necklaces, but the cause of death for the three juveniles wearing backpacks was evenly split between three causes of mortality (Table 3-2).

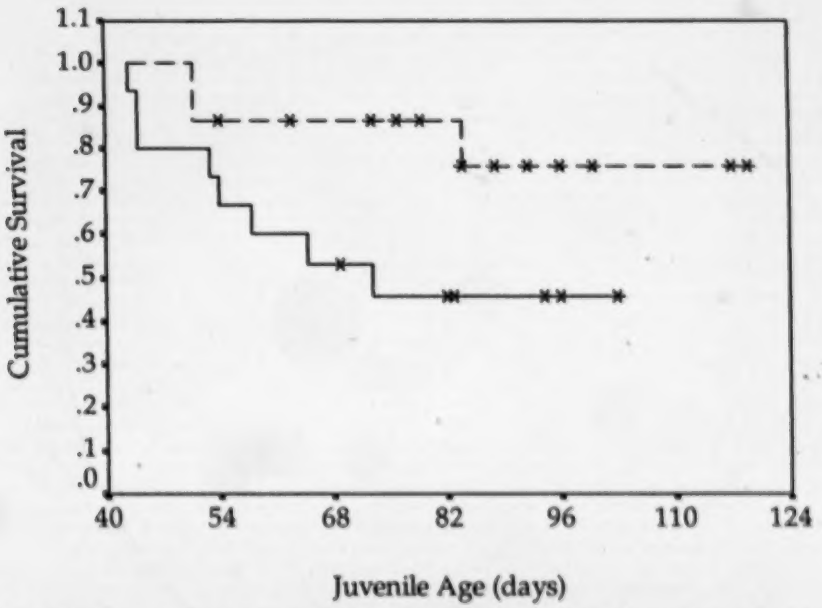

FIGURE 3-2. Cumulative survival functions (1999 and 2000 pooled) of post-fledging sibling juvenile owls wearing either a necklace (solid line, n = 15) or a backpack (dashed line, n = 15) style radio-tag in southern Alberta. Steps down indicate mortality; splice markers (*) indicate censored events.

DISCUSSION

It is important to discern the potential impacts of radio-tags on study animals, principally because researchers have an ethical imperative to ensure tags do not lead to unacceptable negative costs, and practically because the researcher violates the assumption that the tag does not influence survivorship in survival analyses. Significantly lower survivorship of juveniles wearing necklace style tags requires comment.

Concurrent with this study, Todd (2001) studied survivorship of juveniles with the same type of necklace and backpack tags, and found no difference in survivorship between these groups. Because necklaces were used preferentially, at a ratio of 9:1, the probability of detecting a difference in survival between these two groups is remote. No other research has compared the impact of tag style on owl survival.

TABLE 3-1. Average nestling age, mass and body condition at time of capture, and results of *t*-tests comparing these variables between years (A) and between siblings given either a backpack or a necklace style radio-tag (B) in southern Alberta.

A. Nestling Variable	1999 (n = 10)	2000 (n = 20)	*t*	*p*
Nestling Age (days)	38.7 ± 2.29	38.6 ± 0.94	0.48	0.962
Nestling Mass (g)	133.4 ± 1.95	137.0 ± 3.10	-0.78	0.442
Nestling Body Condition (x 10^{-4})	38.65 ± 6.75	34.83 ± 5.98	1.58	0.125
B. Nestling Variable	**Necklace (n = 15)**	**Backpack (n = 15)**	***t***	***p***
Nestling Age (days)	38.2 ± 0.942	39.07 ± 1.72	-0.44	0.661
Nestling Mass (g)	135.7 ± 3.21	135.9 ± 3.01	-0.05	0.964
Nestling Body Condition (x 10^{-4})	35.08 ± 1.22	37.13 ± 2.00	-0.87	0.390

TABLE 3-2. Proportional cause-specific fate of post-fledging sibling juveniles (*n*) wearing either a necklace or a backpack style radio-tag in 1999 and 2000 in southern Alberta.

Tag Style	Survive	Cause of Death			
		Raptor	*Badger*	*Vehicle*	*Unknown*
Necklace (15)	0.467 (7)	0.333 (5)	0.133 (2)	0.000 (0)	0.067 (1)
Backpack (15)	0.800 (12)	0.067 (1)	0.067 (1)	0.067 (1)	0.000 (0)

Radio-tags can increase the risk of mortality by increasing energy demands by damaging the bird or by stripping away insulating feathers. No researchers have reported any apparent physical detriment, such as chafing from the harness, on recaptured owls. Other than the loss of some body feathers underneath the body of the backpack tag, we also did not notice extensive or excessive feather loss on recaptured tagged owls, even on owls returning from migration after wearing a tag for 10 months or multiple years. It does not appear that the proper attachment of radio-tags caused adverse injuries.

Radio-tags can also detrimentally affect birds by increasing energy demands if the tag is too heavy or causes behavioural distractions. Because juveniles are nearly adult size by fledging, the wing load of fledglings is similar to that of adults. Voles are common prey items and can be carried by adult males to the nest at a delivery rate that can reach 24 over a 24 hr period (Poulin 2003), and adult voles can outweigh these radio-tags by a factor of 3 - 15 times (Pattie and Fisher 1999). Therefore, compared to the energetic demands of vole deliveries, it is unlikely that the mass of these tags has excessive negative impacts on short-distance dispersing owls. Radio-tagged owls have returned from migration in subsequent (Clayton 1997, Todd 2001, this study) and several years post-tagging (L.D. Todd pers. comm.), suggesting that for some owls the mass of these tags does not create overly adverse energetic costs during migration. Furthermore, Todd (2001) found no difference in mass between tagged and untagged juveniles recaptured after wearing a tag for many weeks, suggesting that the tag does not limit growth.

Radio-tags can also detrimentally affect birds by increasing aerodynamic energy demands if the tag and antenna are not streamlined with the bird's body. While backpack style tags minimally affect flight aerodynamics because the owls promptly preened the tag and harness straps under the body feathers, necklace tags dangle loosely and increase wind resistance for owls in flight. Additionally, backpacks are situated near the centre of lift of the owl, while necklaces likely affect the balance of the owl in flight because the tag body is shifting around. It

seems likely that necklace style tags contribute to greater energy demands for owls when flying, but I could not discern whether this was responsible for the greater number of mortalities for owls wearing necklaces.

Conway and Garcia (2005) found evidence of tags directly contributing to the mortality of tagged owls, reporting two juveniles that were found dead with a leg caught in the tag harness. The only instance when the tag could potentially be directly related to the death of the owl in this study was when a juvenile was caught by both the necklace antenna and its wing on a barbed-wire fence. Because an untagged juvenile also died after getting caught by its wing on a barbed-wire fence, the barbed-wire fence is the more probable cause of death of the tagged juvenile, not the tag.

Tag failures are frustrating, expensive, and decrease confidence in results. Although all tags were checked for proper operation prior to placement on owls, damaged and disconnected antennae were responsible for 4 of 5 necklace tag failures in this study. Sissons et al. (2001) also report that 6 of 11 adult owls tagged with necklaces failed for the same reason. Because the antenna is more easily accessible on a necklace style tag, it appears that necklace tags are more susceptible to failure than backpack tags. In contrast, Todd (pers. comm.) does not report problems with necklace tags, which is puzzling considering the greater number of identical necklaces utilized.

Tagged birds can be more susceptible to predators (Amstrup 1980, Marks and Marks 1987), and predators are commonly the primary source of mortality for juvenile owls (Todd et al. 2001, Gervais et al. in press, this study). After witnessing a fledgling fly up to challenge a coursing Northern Harrier, I suggest that inadequate predator experience may be related to the high frequency of raptor mortality for juveniles. Further, because necklace tags are more accessible than backpacks, it is feasible that owls with necklace tags spend more time adjusting

the tag, resulting in decreased predator vigilance. I suggest that the higher failure rate of necklace tags also attests to increased interference relative to backpacks.

CONCLUSIONS AND RECOMMENDATIONS

Researchers must ensure that the information gained from tagging animals is greater than the cost of the tag to that individual or population. Furthermore, if tags reduce survival, an assumption of the KM analysis is violated. Although no mortalities could be directly attributed to the tags in this study, the number of tagged individuals was small (and seasonally reduced), and survival rates and sources of mortality were comparable to other studies. Therefore, I cannot conclude that necklace tags are directly responsible for lower survival of juveniles, and the KM assumptions do not appear to be violated. However, the significantly lower survival of juveniles wearing necklace tags relative to those wearing backpacks is of concern.

In contrast to backpacks, necklace tags: 1) had a higher failure rate, 2) had greater aerodynamic drag, 3) were not securely fastened and entailed greater risk of entanglement on vegetation, etc., and 4) may have contributed to decreased predator vigilance. Although backpacks required additional handling time during attachment, the cost to the owls appeared to be less than with necklace tags. I concur with Sissons et al. (2001) and recommend further research into potential negative impacts of different tag styles on Burrowing Owl behaviour. Furthermore, I suggest that this research is most effectively conducted on captive owls in captive breeding facilities. I do not recommend deployment of necklace style tags until the potential negative impacts of these tags are further investigated.

CHAPTER 4

LATE-SEASON DIETS AND JUVENILE PREY USE AND AVAILABILITY

INTRODUCTION

Food abundance and availability affect avian reproductive success and can increase the risk of mortality during periods of food limitation (Newton 1998). Burrowing Owls lay large clutches of eggs irrespective of prey availability (Wellicome 2000), suggesting that population increases will largely be influenced by prey abundances that both reduce starvation of owls and satiate predators (Todd et al. 2003). Burrowing Owls populations also exhibit numerical and functional responses to small mammal (i.e., rodent) abundance (Silva et al. 1995), and prey shortages are related to the starvation of nestlings and juveniles (Gleason and Johnson 1985, Haley 2002, Todd et al. 2001, Wellicome 2000). Tracking prey use provides information that may contribute to the development of practical conservation strategies, but studies of the prey utilized in the northern limit of the breeding range are uncommon (Haug 1985, Schmutz et al. 1991, Sissons 2003, Smith 1981).

Burrowing Owls prey on a diversity of animals from different geographic and trophic guilds. During the breeding season arthropods are typically the most frequently consumed prey items but vertebrates constitute the principal biomass. Insectivory increases in the post-breeding period (e.g., Best 1969, Butts 1973, Desmond 1991, Errington and Bennett 1935, Gleason and Johnson 1985, Green et al. 1993, Green and Anthony 1989, James and Seabloom 1968, Leupin and Low 2001, Lohoefener and Lohoefener 1982, MacCracken et al. 1985, Marti 1974, Maser et al. 1971, Schlatter et al. 1982, Scott 1940, Smith and Murphy 1973, Tyler 1983, Thomsen 1971).

Burrowing Owl foraging activity varies with time of day, type and activity of prey, vegetation structure, substrate, and weather (Butts 1973, Thompson and Anderson 1988) and becomes more nocturnal in the post-breeding period and in

the winter (Best 1969, Butts and Lewis 1982, Gleason 1978, E. Valdez pers. comm.). While insectivory is cathemeral (24-hr) with crepuscular and afternoon peaks, foraging on rodents is principally crepuscular and nocturnal (Poulin 2003). In the northern Great Plains, diurnal foraging should incur greater risk of predation from principally diurnal avian predators, while nocturnal foraging should incur greater risk from principally nocturnal mammalian predators.

Most researchers advocate an opportunistic (i.e., generalist) foraging strategy for Burrowing Owls (Bellocq 1997, Brown et al. 1986, Conroy 1986, Glover 1953, Green et al. 1983, Haug et al. 1993, John and Romanow 1993, Longhurst 1942, Neff 1941, Smith and Murphy 1973, Sperry 1941, Thompson and Anderson 1988, Tyler 1983). Typically these diet studies extrapolate prey availability from casual observations or from prey trapping in generalized habitats. Generally quantifying prey availability may not be representative of prey available in the more localized habitats and micro-habitats being utilized by foraging owls.

In contrast, other evidence indicates more stereotyped (i.e., specialized) foraging through the disproportionate use versus availability of both: 1) rodents (Butts 1973, Gleason 1978, Olenick 1990, Schlatter et al. 1982, Schmutz et al. 1991), and 2) arthropods (Kelso 1938, Butts 1973, Plumpton and Lutz 1993). Further, Kelso (1938), Gleason and Craig (1979), and Green et al. (1993) tracked prey use during grasshopper population irruptions (i.e., when grasshopper prey was essentially unlimited), but other prey items (e.g., vertebrates, beetles, crickets) were more frequent or constituted more biomass in Burrowing Owl diets. Similarly, although reptiles are a greater proportion of diets in the southern deserts (Rodriguez-Estrella 1997), widespread and abundant diurnally active lizards appear to be rarely preyed upon (Schlatter et al. 1980, E. Valdez pers. comm.). Finally, greater diet breadth during breeding (Longhurst 1942, York et al. 2002) and greater insectivory of females than males (Pezzolesi and Lutz 1997, Poulin 2003, York et al. 2002) suggest that dietary specialization may be related to sex or stage of the breeding cycle (Silva et al. 1995).

Opportunistic dietary shifts should emulate prey availability, but the evidence is inconsistent whether Burrowing Owl diets track prey availability. Obstacles to characterizing dietary specialization include: 1) the difficulty of accurately quantifying prey abundances, particularly quantifying ephemerally irruptive prey in localized habitats while they are being exploited by foraging owls, 2) the extrapolation from few pellets or individuals, and 3) the lack of operational methods to quantify the degree of specialization (Sherry 1990).

I tracked radio-tagged post-breeding adults and post-fledging juvenile Burrowing Owls to diurnal roosts in southern Alberta mixed-grass prairie, collected pellets and prey remains and subsequently quantified cohort-specific late-season prey use (i.e., fourth order selection, Johnson 1980). I contrast late-season prey use with breeding season prey use in the same population as Sissons (2003), and with other published late-season diets. Additionally, I tracked post-fledging juveniles to nocturnal foraging sites and tested whether they foraged in areas with greater prey abundances (third order selection, Johnson 1980). I contrast prey available in juvenile foraging sites with the prey in pellet remains to assess the potential for juvenile dietary specialization. I discuss possible mechanisms to explain seasonal variation and dietary heterogeneity between adults and juveniles.

METHODS

Foraging Behaviour

Post-fledging juvenile Burrowing Owl foraging sites were not independent because: 1) dispersing juveniles were accepted into non-natal broods, 2) siblings and adult owls foraged together nocturnally, and 3) a few juveniles did not disperse away from the natal territory or from their parents. Therefore, I defined juvenile habitual foraging sites as localized areas outside of natal territories with at least three temporally independent observations (separate nights) of nocturnally foraging juvenile owls during the post-fledging period. The distance from the

nest to the most distant satellite roost used by adult males during the breeding season demarcated the radii of natal territories.

Reflective tape on leg-bands and a spotlight (Pezzolesi 1994) facilitated observations of radio-tagged owls foraging on or near roads at night. The locations of observed owls were estimated from a hand-held GPS unit, and this point was buffered to a 100 m radius to delineate a foraging location. I also remotely determined the position of radio-tagged nocturnally foraging owls by taking two simultaneous bearings, using the strongest signal to estimate bearing (Springer 1979). An estimated measure of error (± 5°) on each pair of telemetry bearings created error polygons at their intersection (Heezen and Tester 1967, Nams and Boutin 1991), which also delineated foraging locations.

All nocturnal foraging locations were transposed onto a 5 m^2 resolution air-photo, and a 1 ha square representing the sampling area for the prey-trapping grid was positioned to encompass the most area and overlap of the layered foraging locations. Range-control grids were located 1 km in a random cardinal direction from foraging grids. Because localized foraging on roads was commonly observed while tracking foraging juveniles nocturnally in 1999, I also established additional road-control grids in a randomly chosen direction ≥ 1 km from the foraging grids that encompassed high-grade gravel roads (i.e., elevated road with ditches). Corresponding foraging and control grids operated concurrently for three consecutive days between 26-August and 25-September 2000, unless inclement weather postponed trapping.

Prey Use

In 1999 and 2000, burrows in natal territories were cleared of pellets and prey remains prior to fledging. In 1999, pellets and prey remains were collected from all known roost burrows in late September and early October after tagged-owls had migrated away from the study area. In 2000, we attempted to visually and remotely observe tagged owls at diurnal roosts every 3-4 d, and collect pellets

from these roosts every 10 d. I include the final pellets collected on 3-Oct-2000 into the late September fortnight collection because of the reduced number of pellets collected in that period as a result from (e)migrating owls.

Based on observations of owls at diurnal roost burrows, pellets were grouped into four cohorts: 1) post-fledging juveniles, 2) adult females, 3) adult males, and 4) communal. The communal cohort included pellets from roosts where both adult and juvenile owls were observed together, and from roosts with unbanded owls. Monomorphic juvenile plumage precluded categorizing juvenile pellets by sex, but plumage and colour-coded leg-bands helped to visually differentiate adult male and females, and adults from juveniles. Additionally, colour-coded reflective tape on leg-bands and a one million candle power spotlights allowed us to differentiate adults from juveniles at night.

Pellets were dissected by hand and undigested prey components (e.g., bones, chitin) were used to enumerate and identify prey ingested (Marti 1974). If pellets were found crumbled, a common occurrence for pellets primarily composed of invertebrates, the number of pellets was estimated. By pairing jawbones and comparing dental bone fragments in pellets with a reference collection (loaned by the University of Alberta Zoology Museum), I identified and enumerated mammalian prey items, while feathers found in pellets and at roost burrows were used to enumerate songbird prey items. Beetles (Coleoptera) were enumerated by counting head capsules, while obvious physical characteristics such as mandibles, colour, and patterning of elytra grouped these into families. Grasshoppers (Acrididae) and crickets (Gryllidae) were separated and enumerated by mandible pairs. Although Burrowing Owls consume prey items that may not be represented in prey remains and pellets because they are completely digested or crushed (e.g., moths), I assume that the prey remains collected and identified in pellets relatively represent primary prey as identified during the breeding season for this population (Sissons 2003).

Prey Use Data Analysis – Prey items identified in pellets and from remains located at burrows and roosts were first broadly pooled into three major prey orders: 1) Vertebrates, 2) Orthopterans (Acrididae and Gryllidae) and 3) Coleopterans. Subsequently, prey items were categorised into nine minor prey groups: 1) rodents (Cricetidae (new world mice), Muridae (old world mice) and Sorcidae (shrews)), 2) passeriformes (songbirds), 3) Acrididae, 4) Gryllidae, 5) Carabidae (ground beetles), 6) Scarabidae (scarab beetles), 7) Silphidae (carrion beetles), 8) Tenebrionidae (darkling beetles), and 9) unknown beetles. Except for rodents, I did not attempt a lower taxonomic level of identification than prey group, and therefore do not compare niche-breadth measures among or between cohorts.

I assume that the frequency of prey in pellets is representative of consumption and capture frequency, and that biomass is more indicative of the nutritional, caloric, and energetic benefit of prey items. Prey frequencies were standardised into percentages for individuals in the juvenile and adult cohorts, and for the nearest natal territory for the communal cohort. Because of the multiple magnitudes difference in prey masses, for example a rodent can be 150 times the mass of a ground beetle, frequencies underestimate the contribution of larger prey items and overestimate the contribution of frequently consumed but substantially smaller prey items. I estimated prey biomass by multiplying the total abundance of each prey group by the respective average mass (Table 4-1), and standardised this net biomass into percentages for individual adults and juveniles, and the nearest natal territories for the communal cohort.

Average prey frequency and biomass measures among cohorts were not normally distributed. Therefore I compared these measures using Kruskal-Wallis tests, and if a significant difference ($P \leq 0.10$) was found, Mann-Whitney U tests were subsequently applied between cohorts. Additionally, to illustrate seasonal prey-use variation, principal prey groups were pooled by the date of collection over the first and last half of each month.

TABLE 4-1. Estimated prey mass and sources used to calculate biomass of prey items in pellets.

Prey Group	Mass (g)	Source
Vertebrates		
Lagurus curtatus	30.0	Steenhoff 1983
Peromyscus maniculatus	17.9	This study
Microtus pennsylvanicus	25.0	Sissons 2003
Mus musculus	22.0	Marti 1974
Unidentified Rodents	22.0	Sissons 2003
Soricidae	6.0	Steenhoff 1983
Passeriformes	30.0	Marti 1974
Orthoptera		
Acrididae	0.6	Marti 1974
Gryllidae	0.4	Marti 1974
Coleoptera		
Carabidae	0.2	Marti 1974
Scarabidae	0.3	Marti 1974
Silphidae	0.3	Marti 1974
Tenenebrionidae	0.6	Marti 1974
Unknown beetle	0.2	Estimated

Prey Availability

Prey-trapping grids were comprised of nine stations (3 x 3), each 50 m apart. Each station included a Tin Cat™ repeating mousetrap to live-capture rodents, a round 13 cm diameter pitfall trap (Spence and Niemela 1994) to capture ground beetles, crickets and shrews, and a 0.25 m^2 square frame (Onsager and Henry 1977) from which flushing grasshoppers were enumerated. Pitfall traps and flushing frames were each placed 5 m to the east and west from the centre mousetrap at each station. These grids were established in three sites: 1) nocturnal foraging sites, 2) range-control sites, and 3) road-control sites (see Foraging Behaviour).

Vertebrate Prey Availability – Mousetraps were baited with peanut butter, black-oil sunflower seeds and carrot slices, to attract and sustain captured rodents,

three nights prior to commencement and throughout the duration of trapping. Mousetraps were set and checked within 1.5 hr of sunset and sunrise, and trapping was postponed if the overnight temperature was forecast < 5°C. Captured rodents were identified, marked with individually numbered ear tags, and released at the point of capture. The abundance of songbirds was not quantified.

Invertebrate Prey Availability – Pitfall traps did not have a killing solution and were not baited or covered, but funnels discouraged escapes and scavenging. Because ambient weather conditions can reduce invertebrate motility and capture rates (Greenslade 1964), pitfall traps in foraging and corresponding control grids were always operated on the same days for the same duration, and were closed if ambient overnight temperatures were forecast < 5°C or if substantial precipitation was predicted. To identify terrestrial arthropod diel activity schedules, pitfall traps were open 24-hr, unless the climate constraints precluded trapping, and were cleared of captures ≤ 1.5 hr before sunset and after sunrise. Entomologists at the University of Alberta identified Carabid beetles while beetles from other families were identified by comparison with specimens at the E.A. Strictland Entomology Museum, where a taxonomic series is deposited.

Grasshoppers were counted between 13:00 - 16:00 as they flushed from the square frames, starting when the enumerator was 10 m from the frame, and ending as we brushed our hands through the grass inside the frames to ensure that all of the grasshoppers flushed. Counts were postponed if: a) ambient temperature was < 15°C, b) average wind speed was > 20 kph, or c) if there was > 50% cloud cover.

Prey Availability Data Analysis – Prey data were not normally distributed, therefore non-parametric tests were used. All analyses were conducted using SPSS software (SPSS 1999) and, unless otherwise stated, results are presented as mean ± SE. Because of the relatively small number of prey-trapping grids and the

high variability in the number and diversity of arthropods captured, significance was assessed at $\alpha \leq 0.10$.

Indices of relative rodent abundance were calculated for new captures per 100 trap nights for each grid over the three night trapping period. Rodent abundance indices were compared among prey-trapping grids using a Kruskal-Wallis test. The number of grasshoppers flushed from frames was averaged for each grid, standardized into mean density per square meter, and also compared among grids using a Kruskal-Wallis test. No attempt was made to identify grasshoppers as they flushed.

Terrestrial arthropods captured in pitfall traps were grouped by taxonomic Order and Family, except for beetles in the predominant family (Carabidae); these were pooled by Tribe. To compare the relative abundance of arthropods between grids, I summed those captured in pitfalls for each grid, and averaged among the three grid types (i.e., foraging, road, control). I excluded prey groups from statistical analyses if < 5 individuals were captured. I assumed that capture frequencies represented the relative abundance of these prey groups in the prey-trapping grids. The clearing of pitfall traps in mornings and evenings allowed for evaluation of arthropod activity schedules, and permitted analysis of prey data from the nocturnal period when juveniles were utilizing foraging sites. To compare arthropod prey activity in foraging and control sites, I summed the number captured in pitfalls for the total sample (i.e., both diurnal and nocturnal captures) and for the nocturnal captures only.

I compared the relative abundance of terrestrial arthropods between foraging and control grids using Mann-Whitney U tests. Further, I compared average prey group ranks for both the total sample and the nocturnal sub-sample between foraging and range-control grids using the program PREFER, a method that is robust whether infrequent items are included or excluded in the analysis, and when measurements are not exact (Johnson 1980). Because PREFER constrains

the number of components (prey groups) by the number of individuals (grids), this method was unsuitable for the four road-control grids. Therefore, Mann-Whitney U tests were used to compare prey group abundance between foraging and road-control grids.

Prey habitat associations were explored by pooling the total number of beetles, crickets, and rodents captured in the apparently distinct habitats of each trapping station, and standardizing by the total number of traps in each habitat type. Because grasshoppers were not collected, the number counted flushing from frames were averaged for each habitat type. Although trap stations were designed to compare the relative abundance of prey between foraging and control sites, not to equally sample habitat types, I assume there was a sufficient number of stations to broadly illustrate typical prey group habitat preferences.

RESULTS

Foraging Behaviour

Adult and juvenile dispersal behaviours were variable. Post-breeding adults became independent of breeding territories and independently used a single area for roosting. In contrast, post-fledging juveniles tended to disperse periodically to new roosts until migration, and some of these roosts housed many individuals. Although some adults were observed with juveniles foraging in sites near natal territories in initial stage of fledging (i.e., late July and early August), most owls roosted independently by mid-August.

Juveniles departed diurnal roosts (see Figure 1-3) at dusk, flying to foraging sites where they were frequently observed ground foraging. Occasionally juveniles were observed using short perches (< 2 m) such as fence-posts and energy industry structures (e.g., a flare stack pipe and support wires) when foraging. Although we did not track individual owls for extended periods of the night, on a few occasions we tracked individual juveniles and siblings from one habitual

foraging site to another > 1 km away. Nocturnally foraging adult owls were not tracked.

Nocturnal tracking of foraging juveniles from mid-August to early September yielded nine habitual foraging sites, frequented by 11 juveniles (including four sibling pairs). These sites were located an average distance of 1595 ± 757 m (range 195 – 7370 m) from the seven originating natal burrows (see Figure 1-3). Ephemeral wetlands were associated with 67% of the habitual foraging sites. All habitual foraging sites encompassed, or were adjacent to, some type of surface disturbance where the prairie vegetation has been reduced or removed, such as gravel roads, tire-track beds, dugouts, firebreaks, and energy industry well-pads. Prey-trapping grids in habitual foraging sites were dispersed around the study area (see Figure 1-3); the closest foraging grids were > 550 m apart and all others were > 1 km apart. One range-control grid was randomly placed in a fallow, non-irrigated, winter-wheat stubble field, but all other range-control grids were located in the upland native prairie habitat or a mixture of habitat types.

Prey Use

During the initial period of fledging, a few individual and sibling juveniles were gregarious – foraging together and dispersing into non-natal nesting territories many kilometres away from their natal territories, or moving into communal roosting burrows occupied by non-sibling juveniles and other unbanded owls. Because mortalities and dispersal movements confounded tracking of all tagged owls to diurnal roosts for pellet collections (see Chapter 2), the juvenile cohort ultimately included four sibling pairs, and the adult cohort included three post-breeding pairs. The total number of pellets collected was 72 (5.5 ± 1.1) for the 13 post-fledging juveniles, 42 (9.5 ± 2.6) for the four adult females, 38 (10.5 ± 3.6) for the four adult males, and 120 (15.0 ± 5.5) at the eight communally attended roosts. I did not categorise all owls utilizing the communal roosts, but nearly 41% of pellets collected at communal roosts were from an adult female and a member

of her brood sharing the same roost burrows on the edge of their natal territory until migration.

A total of 4773 prey items were identified in pellets and prey remains from 1999, while 7496 prey items were identified from prey remains and in pellets collected 8-August to 3-October 2000. From 1999 to 2000 the use of vertebrate and grasshopper prey was reduced, but beetle and cricket use increased (Table 4-2). Because the collected pellets could be attributed to identifiable cohorts in 2000, but not in 1999, subsequent results and discussion focus on the 2000 late-season diets.

Vertebrate Prey Use –Sixty-two percent of the rodents in pellets were identified by dental fragments. Deer mice (*P. maniculatus*) were most frequent, and were identified in the pellets of all cohorts except juveniles. Meadow voles (*M. pennsylvanicus*) were found in pellets from all cohorts except adult females. Sagebrush voles (*L. curtatus*) and shrews (*Sorex* spp.) were found in the diet of all cohorts except for the juvenile cohort. The two house mice found each year may have been provisioned during trapping. All rodent species were present only in pellets collected at communal roosts. In terms of biomass, both the vertebrate prey order and the rodent prey group were significantly greater in both the adult male and female cohorts than in the juvenile cohort (Table 4-3).

Songbird remains were found only at adult female and communal roosts. Songbirds are a relatively minor component in the diets of continental owls in contrast to resident island populations in the Caribbean (Wiley 1998).

Although the utilization of vertebrates was less in 2000 compared to 1999, prey populations were not monitored annually and it is unclear whether this trend results from the increased effort locating juvenile pellets or from reduced vertebrate abundances related to the severe drought in 2000.

TABLE 4-2. Total percent frequency and total percent biomass of late-season Burrowing Owl prey identified in remains and pellets from 1999 (n = 148) and 2000 (n = 272) in southern Alberta.

PREY ORDER Prey Group Family/Species	Percent Frequency 1999	 2000	Percent Biomass 1999	 2000
VERTEBRATES	**2.1**	**0.9**	**42.4**	**32.9**
Lagurus curtatus	0.3	0.1	8.3	5.5
Peromyscus maniculatus	0.8	0.2	16.5	5.7
Microtus pennsylvanicus	0.1	0.1	2.3	4.6
Mus musculus	<0.1	<0.1	0.5	0.5
Sorex spp.	0.5	0.1	3.5	1.0
Unknown Mouse	0.3	0.3	7.1	12.1
Passeriformes	0.1	0.1	4.2	3.4
INVERTEBRATES	**97.9**	**99.1**	**53.5**	**63.7**
Coleoptera	**25.9**	**60.8**	**6.8**	**27.6**
Carabidae	22.3	46.4	4.9	16.0
Scarabidae	<0.1	<0.1	<0.1	<0.1
Silphidae	1.4	2.2	0.5	1.1
Tenebrionidae	2.1	9.1	1.4	9.4
Unknown Beetles	0.2	3.0	<0.1	1.0
Odonata	**<0.1**	**-**	**<0.1**	**-**
Orthoptera	**71.9**	**38.3**	**46.7**	**36.1**
Acrididae	68.3	28.4	45.1	29.3
Gryllidae	3.7	9.8	1.6	6.8

Invertebrate Prey Use – Arthropods were the most frequently consumed prey items and contributed the majority of biomass to late-season diets in both years (Table 4-2). Ground beetles and grasshoppers were respectively the most frequently consumed arthropods by all cohorts. Crickets and darkling beetles were next most frequent, but crickets were ranked third for adults whereas darkling beetles were ranked third for the juvenile cohort (Table 4-3). Dietary disparity is exemplified by differences in arthropod biomass between juveniles and adults – juvenile diets were composed almost exclusively of invertebrate prey whereas invertebrates contributed approximately 60% of biomass in adult diets (Table 4-4). Despite this disparity, the greater biomass of beetles in juvenile diets over adult females was the only significant difference in arthropod use. Because of the mixture of adult and juvenile owls attending communal roosts, prey use

identified in the diet of the communal cohort appeared intermediate between adult and juveniles.

Horsehair worms (Nematomorpha; Dictophymoidea), parasites that hatch and consume infected arthropods, were found in pellets at 67% of roosts in 1999, and 46% of roosts in 2000. In terms of individual owls tracked in 2000, 50% of adults, and 54% of juveniles had nematodes present in pellets. Notably some pellets appeared to consist entirely of horsehair worms. Although horsehair worms are not believed to parasitise vertebrates, they remain undigested in the crop of the owls, suggesting that they could potentially reduce the nutritional and energetic benefit of host arthropods consumed by foraging owls. It is unknown if horsehair worms can substantially reduce arthropod abundance by increasing mortality rates. One horsehair worm was found in the body cavity of a darkling beetle (*Eleodes hispilabris*) in a pellet, but they were most frequently encountered in the body cavity of field crickets collected in pitfall traps, suggesting multiple vectors for consumption by Burrowing Owls. I am unaware of any other reports of horsehair worms in raptor pellets.

Seasonal Prey Use – While beetle and grasshopper prey use varied substantially between fledging and migration, only grasshopper and cricket biomass continuously increased through the late-season (Table 4-3). Although rodents were almost half of August dietary biomass, the consumption of rodents became considerably diminished by early September when grasshoppers and ground beetles were principal components of dietary biomass.

TABLE 4-3. Total percent biomass of vertebrate and invertebrate prey from pellets pooled over two week intervals in southern Alberta.

	Vertebrate Prey		Invertebrate Prey				
Time Period (pellets)	Rodents	Songbirds	Grass-hoppers	Crickets	Ground Beetles	Darkling Beetles	Other Beetles
Early August (n = 62)	40.9	2.7	17.7	5.0	16.9	14.9	1.8
Late August (n = 76)	45.7	0.0	27.2	5.0	10.4	10.1	1.6
Early September (n = 65)	9.1	10.2	32.1	8.8	29.7	5.0	5.1
Late September (n = 69)	22.2	2.9	47.0	10.1	12.3	4.2	1.2

Prey Availability

Trapping Summary – Mousetraps were closed during daytime, but were set for a total of 243 trap-nights in foraging and range-control grids, and 108 trap-nights in road-control grids. The collections of arthropods captured in pitfall traps was conducted for a total of 243 trap-days and 243 trap-nights in foraging and range-control grids, and 108 trap-days and 108 trap-nights in road-control grids. Grasshoppers were counted as they flushed from a total area encompassing 60.75 m^2 in the foraging and range-control grids, and 27 m^2 in road-control grids.

In addition to carrion beetles ($n = 8$), which were excluded from analyses because pitfall traps did not contain the requisite bait (i.e., olfactory attraction), the following prey groups were eliminated from analyses because < 5 individuals were captured: Dermestidae ($n = 3$), Histeridae ($n = 3$), and ground beetles from Tribe Agonini ($n = 2$) and Tribe Bembidiini ($n = 1$).

Vertebrate Prey Availability – Although owls preyed upon at least five different small mammals, only deer mice ($n = 174$ new captures) were captured in mousetraps. Deer mouse relative abundance was somewhat greater in foraging grids (Figure 4-2), but is not significantly different among grids ($x^2 = 0.222$, df = 2, $P = 0.895$). Only a single shrew was captured in a pitfall trap in a range-control grid.

Invertebrate Prey Availability – Grasshopper densities (Figure 4-3) were low on all prey-trapping grids, but differed significantly among grids ($x^2 = 5.378$, df = 2, $P = 0.068$). Grasshopper density at road-control grids (4.07 ± 0.35 per m^2) was significantly greater (U = 0, $P = 0.029$) than at range-control grids (2.09 ± 0.51 per m^2), but foraging grids density (2.40 ± 0.46 per m^2) was not different from range-control (U = 34, $P = 0.605$) or road-control grids (U = 2.0, $P = 0.1114$).

In total, 944 beetles (37 species in 7 families identified) and 255 crickets were captured in the pitfall traps. Most crickets (71%) were captured diurnally, while most beetles (63%) were nocturnal captures (Figure 4-3). Although larger bodied beetles have a higher probability of falling into pitfall traps (Andersen 1995), smaller ground beetles dominated (75%) the collection. Indeed, two small (< 1 cm) ground beetles, *Harpalus amputatus* (36%) and *Amara obesa* (17%), together comprise more than half the total number of beetles collected from pitfall traps.

Significantly more arthropods were captured in pitfall traps in foraging grids than in field-control grids for both the total ($U = 19$, $P = 0.063$; Figure 4-4.A) and nocturnal collections ($U = 19$, $P = 0.063$; Figure 4-4.B). In contrast, there was no difference in arthropod capture frequency between the foraging and road-control grids for either the total catch ($U = 4$, $P = 0.343$) or the nocturnal captures only ($U = 4$, $P = 0.343$). When prey group ranks were compared using the program PREFER, capture frequencies for both the total catch ($F_{(8,1)} = 0.882$, $W_{(K=50)} = 1.87$, and the nocturnal catch ($F_{(8,1)} = 1.10$, $W_{(K=50)} = 1.94$) indicate significant ($\alpha \leq 0.10$) differences between foraging and range-control grids (Table 4-5.A and 4.5.B).

Rank differences indicate that Harpalini beetles and crickets were more frequently captured in foraging grids than in range-control grids, and respectively these prey were the highest ranked groups for both the total and the nocturnal catches (Table 4-5). Tribe Harpalini consisted principally (94%) of one species, *Harpalus amputatus*. Pterostichini and Scaritini, two predominantly diurnal Tribes more frequently captured in foraging sites, were ranked third and fourth respectively for the total sample, but the principally nocturnal Tribe Amarini replaced these as the final (third) group more frequently captured in foraging grids for the nocturnal sub-sample. Similar to Harpalini, Tribe Amarini was also dominated (83%) by one species, *Amara obesa*.

TABLE 4-4. Percent frequency and rank of prey orders and groups from pellets and remains collected at post-breeding adult, post-fledging juvenile, and communally attended diurnal roosts, from August to October, 2000, in southern Alberta. The communal cohort was excluded from statistical tests ($\alpha \leq 0.10$) among and between cohorts, but is presented to illustrate that the communal diet is intermediary between adults and juveniles.

Prey Order	Juveniles		Adult Males		Adult Females		Communal Roosts		P	x^2
Prey Group	Frequency	Rank	Frequency	Rank	Frequency	Rank	Frequency	Rank		
Vertebrates	**0.06 ± 0.04**	**3**	**2.15 ± 1.00**	**2**	**1.42 ± 0.52**	**3**	**1.31 ± 0.67**	**3**	**0.82**	**0.40**
Rodents	0.06 ± 0.04	7	2.15 ± 1.00	6	1.12 ± 0.44	4	1.27 ± 0.67	6	0.82	0.40
Passeriformes	0	8	0	8	0.30 ± 0.19	7	0.04 ± 0.03	8	1.00	0.00
Orthoptera	**31.66 ± 7.60**	**2**	**45.05 ± 6.36**	**1**	**57.82 ± 16.72**	**1**	**42.47 ± 10.00**	**2**	**0.88**	**0.26**
Acrididae	27.83 ± 7.56	2	28.27 ± 6.87	2	42.11 ± 19.80	2	34.63 ± 7.55	2	0.81	0.43
Gryllidae	3.83 ± 2.06	6	16.78 ± 5.69	3	15.71 ± 9.43	3	7.89 ± 3.67	4	0.17	3.60
Coleoptera	**68.28 ± 7.59**	**1**	**52.80 ± 7.04**	**1**	**40.76 ± 16.74**	**2**	**56.21 ± 9.69**	**1**	**0.88**	**0.26**
Carabidae	48.37 ± 7.56	1	35.58 ± 5.97	1	28.02 ± 11.83	1	47.29 ± 9.16	1	0.88	0.26
Scarabidae	0	8	0	8	0	8	0.13 ± 0.13	9	-	-
Silphidae	3.31 ± 1.29	4	2.53 ± 0.63	5	1.22 ± 0.65	6	1.89 ± 0.66	5	0.29	2.49
Tenebrionidae	9.23 ± 2.83	3	10.75 ± 3.87	4	8.36 ± 4.75	3	6.54 ± 1.53	3	0.60	1.03
Unknown Beetles	7.37 ± 3.53	5	3.94 ± 3.80	7	3.16 ± 2.90	5	0.35 ± 0.33	7	0.17	3.60

TABLE 4-5. Percent biomass and rank of prey orders and groups from pellets and remains collected at post-breeding adult, post-fledging juvenile, and communally attended diurnal roosts, from August to October, 2000, in southern Alberta. The communal cohort was excluded from statistical tests ($\alpha \leq 0.10$) among and between cohorts, but is presented to illustrate that the communal diet is intermediary between adults and juveniles.

Prey Order	Juveniles		Adult Males		Adult Females		Communal Roosts		P	x^2
Prey Group	Biomass	Rank	Biomass	Rank	Biomass	Rank	Biomass	Rank		
Vertebrates	**3.35 ± 2.56^{AB}**	**3**	**42.16 ± 13.17^{A}**	**1**	**40.67 ± 10.02^{B}**	**1**	**27.37 ± 9.54**	**2**	**<0.01**	**3.61**
Rodents	3.35 ± 2.56^{AB}	7	42.16 ± 13.17^{A}	1	30.31 ± 5.80^{B}	1	25.63 ± 9.34	3	<0.01	14.11
Passeriformes	0	8	0	7	10.36 ± 6.91	6	1.74 ± 1.16	7	0.01	8.93
Orthoptera	**43.05 ± 8.27**	**2**	**33.13 ± 6.45**	**1**	**41.52 ± 11.37**	**1**	**43.51 ± 10.02**	**1**	**0.82**	**0.39**
Acrididae	38.57 ± 8.19	2	22.48 ± 4.93	1	29.68 ± 12.24	2	37.74 ± 8.17	1	0.73	0.64
Gryllidae	4.48 ± 2.45	5	10.65 ± 4.13	3	11.84 ± 8.92	5	5.77 ± 2.75	5	0.12	4.24
Coleoptera	**53.60 ± 7.86^{A}**	**1**	**24.71 ± 8.45**	**2**	**17.81 ± 8.17^{A}**	**2**	**29.13 ± 9.56**	**3**	**0.03**	**0.71**
Carabidae	31.13 ± 6.49	1	13.19 ± 5.80	2	7.93 ± 3.12	4	21.78 ± 9.20	2	0.80	5.05
Scarabidae	0	8	0	7	0	9	0.02 ± 0.02	9	-	-
Silphidae	2.40 ± 0.87	4	1.10 ± 0.37	5	0.68 ± 0.47	8	0.78 ± 0.25	6	0.58	1.09
Tenebrionidae	14.92 ± 4.04	3	8.18 ± 1.91	4	7.77 ± 4.08	3	6.42 ± 0.87	4	0.63	0.92
Unknown Beetles	5.15 ± 2.71	6	2.24 ± 2.22	6	1.42 ± 1.37	7	0.13 ± 0.12	8	1.00	0.00

^{AB} The same superscript letter along a row indicates a significant difference between cohorts ($P \leq 0.10$).

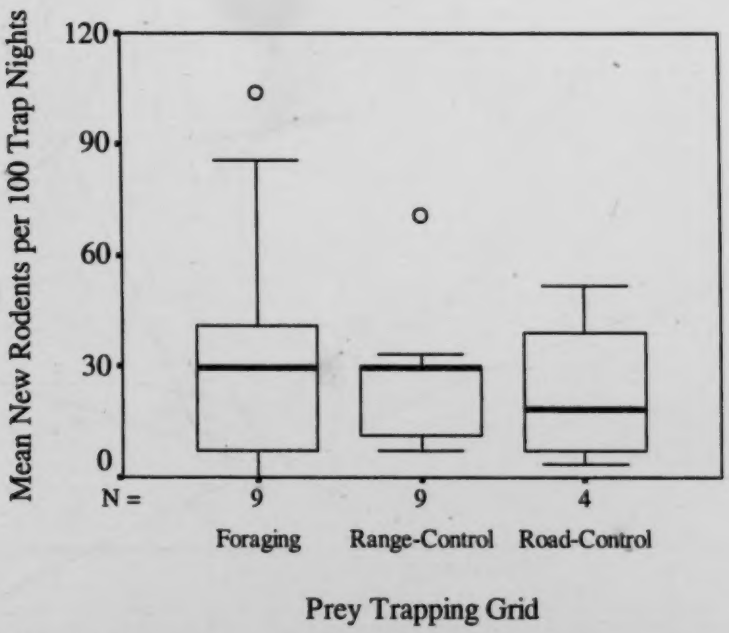

FIGURE 4-1. The relative abundance of deer mice in foraging, range-control, and road-control prey-trapping grids in August and September, 2000, in southern Alberta.

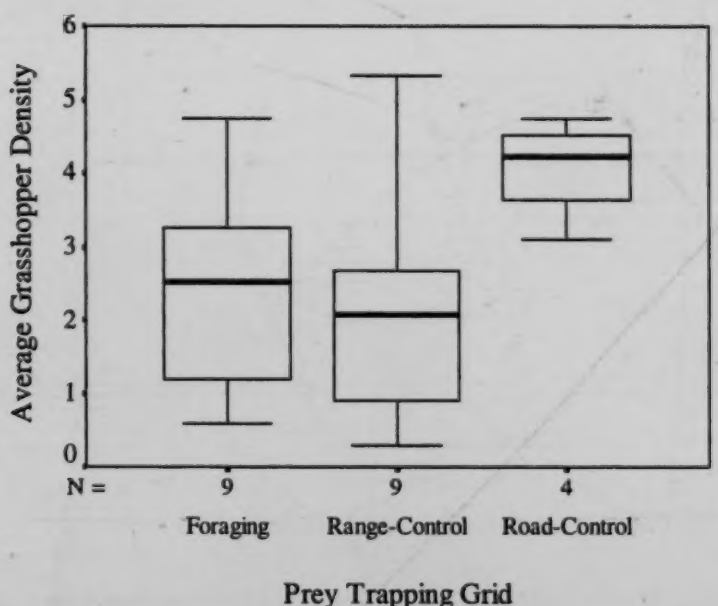

FIGURE 4-2. The average density (per m^2) of grasshoppers in foraging, range-control, and road-control prey-trapping grids in August and September, 2000, in southern Alberta.

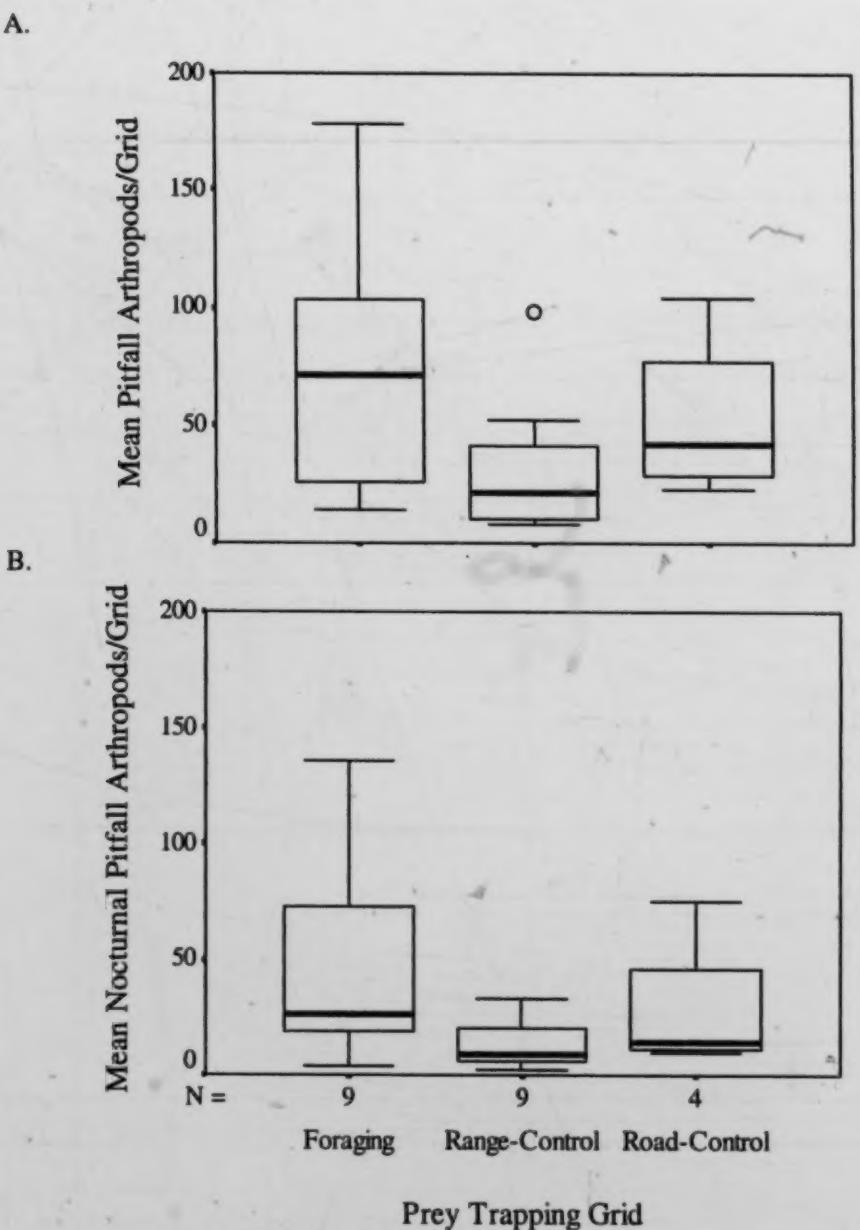

FIGURE 4-3. Box plots illustrating the total (A) and nocturnal (B) average abundance of arthropods captured in pitfall traps in foraging, range-control and road-control grids, in southern Alberta.

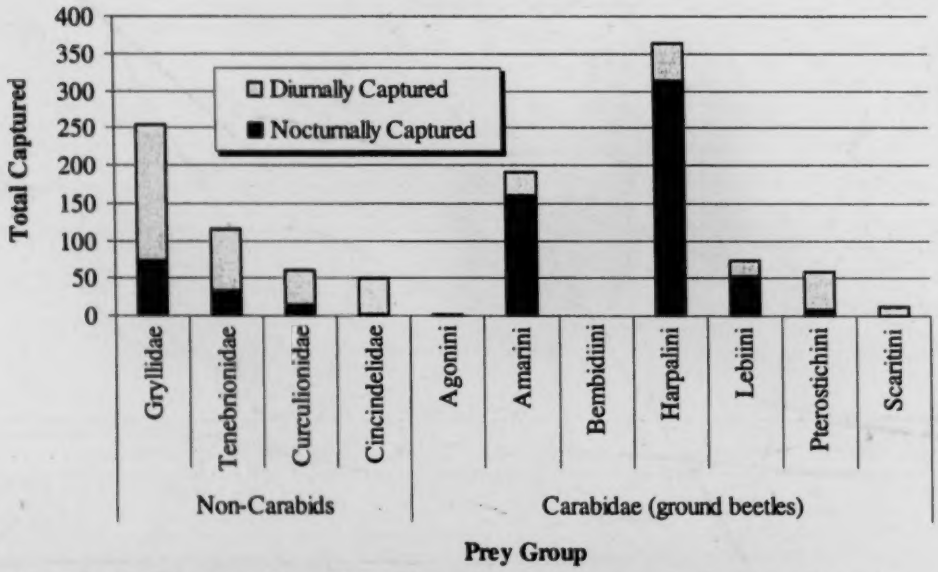

FIGURE 4-4. Total number of diurnal and nocturnal arthropods captured in all trapping grids in August and September, 2000, in southern Alberta. Taxonomic family pools arthropods, except for Carabid beetles which are pooled by tribe.

TABLE 4-6. Prey group ranking, and average rank difference between foraging grids and range-control grids, for both total captures (A) and the subset of nocturnal captures (B) between August and September, 2000, in southern Alberta. Prey groups are ranked from the most (1) to the least (9) frequently captured in pitfall traps. A negative rank difference indicates higher capture frequency in foraging grids. Prey groups with the same superscript letter significantly differ ($\alpha \leq 0.10$).

	A) Total Arthropods		B) Nocturnal Arthropods	
Rank	Prey Group	Rank Difference	Prey Group	Rank Difference
1	Harpalini^{ACDH}	-2.06	Harpalini^{B}	-1.67
2	Gryllidae^{E}	-1.00	Gryllidae	-0.88
3	Pterostichini^{ABF}	-0.72	Amarini^{A}	-0.66
4	Scaritini^{G}	-0.11	Cincindelidae	0.11
5	Amarini^{I}	-0.06	Pterostichini	0.22
6	Cincindelidae	0.16	Curculionidae	0.44
7	Tenebrionidae^{BC}	1.00	Tenebrionidae	0.61
8	Lebiini^{D}	1.33	Lebiini	0.83
9	Curculionidae^{EFGHI}	1.44	Scaritini^{AB}	1.00

Darkling beetles were the only prey group captured on all foraging and range-control grids. Amarini beetles were the only prey group present on all nine foraging grids, whereas Harpalini beetles and crickets were present at all but one foraging grid. All other arthropod prey groups were captured at ≤ 5 grids.

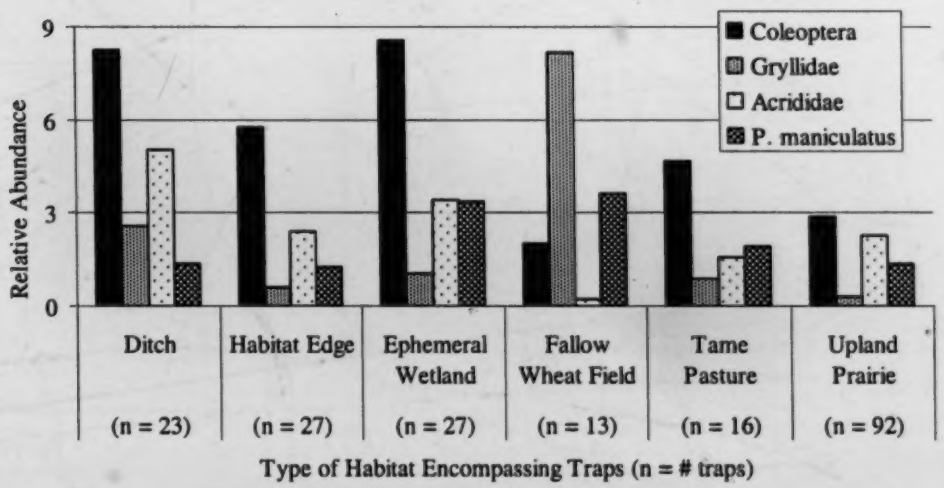

FIGURE 4-5. Prey guild habitat associations illustrated by the relative abundance (#/trap) of prey from the four principal groups, grouped by the apparently distinct habitats surrounding traps, in southern Alberta. Habitat edges include apparent edges between upland prairie and tame pasture, ephemeral wetlands edges, and vehicle tire-beds. Note that trapping effort is not equal in all habitat types.

High arthropod capture rates (> 1 per trap) at some of the prey-trapping grids are suggestive of aggregation densities, and were attained in six foraging grids, two range-control grids, and one road-control grid (Appendix I). Notably, *H. amputatus* were captured at a rate > 4 per trap in three foraging grids, a rate unmatched by any other arthropod group. Crickets and Pterostichini beetles were also captured at rates > 1 per trap in foraging grids, but crickets were captured at a rate > 3 per trap in the single range-control grid that was situated in a stubble wheat field. *A. obesa* attained capture rates > 1 per trap in control grids, but not in

any foraging grids. No other prey groups attained capture rates > 1 per pitfall trap.

Notably, the predominant upland prairie habitat harboured the lowest abundances of two primary prey used by juvenile owls; ground beetles and crickets (Figure 4-6). The relative abundance of prey groups in the apparently distinct habitats suggest that: 1) beetles and grasshoppers were most abundant in ephemeral wetlands and ditches, 2) crickets were most abundant in fallow wheat fields and ditches, and 3) deer mice were most abundant in fallow wheat fields and ephemeral wetlands.

DISCUSSION

I tracked post-breeding adult and juvenile owls to diurnal roosts, where I collected pellets and prey remains to assess late-season diets in the northern periphery of breeding range. Additionally, I tracked juveniles to nocturnal foraging sites, and trapped prey in foraging and randomly located control sites to assess: 1) whether juvenile owls forage in areas with greater prey abundance, and 2) if prey communities in foraging sites are distinct.

Consistent with most investigations of Burrowing Owl diets, invertebrates were the most frequently consumed prey items in southern Alberta, but vertebrates contributed much less biomass to late-season diets than is typically reported during breeding. Seasonally increasing insectivory has been previously observed, but is particularly apparent in this population in 1999. I discuss potential reasons for seasonally increasing insectivory in Burrowing Owls with respect to ecological and evolutionary mechanisms.

Ecological Mechanisms

Ecological mechanisms for seasonally increasing insectivory include: 1) the effect of weather, 2) seasonal vegetation growth obscuring and protecting rodents (Errington and Bennett 1939, Green and Anthony 1989) and 3) differential prey

availability as a result of prey population irruptions or seasonal population increases (Butts 1973, Gleason 1978, Green et al. 1993, Green and Anthony 1989, Grimm et al. 1985, Lohoefener and Lohoefener 1982, Silva et al. 1995).

Effect of Weather – The severe drought in 2000 may have negatively impacted rodent populations, and reduced prey availability, but rodents supplied less than half of late-season dietary biomass in 1999 when precipitation was above normal. Additionally, rodents were trapped on > 90% of grids, suggesting deer mice were widespread in the study area. It appears that the trend for increasing insectivory in this study occurred despite the effect on rodents of disparate annual precipitation.

Arthropod activity is restricted by low temperatures, and inactive or sheltering arthropods are less available to foraging owls. This relationship is illustrated by reduced use of ground beetles in late September when minimum temperatures decline to freezing. Similarly, grasshopper activity was greatest during the hotter times of the day (Abrams and Pearson 1982, Carruthers et al. 1992), and grasshopper biomass in owl diets appears to track this temperature constraint: reduced grasshopper frequency in early September when maximum daily temperatures were typically < 20°C, is followed by increasing grasshopper frequency in late September diets when the majority of daily maximums are > 20°C. Other than ambient temperature affecting arthropod activity and ultimately juvenile foraging success, I do not know of alternate reasons to explain the oscillating frequency of ground beetles and grasshoppers in juvenile diets.

Vegetation Obstruction – Vegetation obstruction does not appear to be an adequate explanation for seasonally increasing insectivory because rodents continue to decrease in late-season diets after rangeland vegetation growth has generally stabilized (Green 1983), and rodent trapping indicates that deer mice were widely available in the late-season. Further, reasons other than vegetation

obstruction must explain seasonally increasing insectivory in 2000, because the drought prevented plant growth throughout the growing season and terrestrial prey were not concealed by dense or tall vegetation on the dry prairie.

Differential Prey Availability – Substantial seasonal increases and/or arthropod population irruptions in the late summer may have provided the conditions appropriate for increasing insectivory in late-season owl diets. For example, Butts (1973) and Green (1983) report the only other Burrowing Owl diets with a similar level of insectivory, and note that grasshoppers were 'very numerous' or at 'epidemic populations' (i.e., $\geq 40/m^2$). In this study, increasing grasshopper dietary biomass in late-season diets is not a consequence of extraordinary abundances as shown by both annual monitoring of grasshopper populations in the vicinity of the study area (D. Johnson pers. comm.), and the low grasshopper population densities found in prey grids in this study.

Beetle populations are also irruptive, but these specific increases are typically restricted to habitats that provide the appropriate environmental conditions (Fadl and Purvis 1998, French et al. 2001, Miller 2000). Higher densities of *H. amputatus* and crickets in juvenile foraging sites suggest localized prey aggregations relative to other arthropod prey groups. Furthermore, these foraging sites were sought out by nocturnally foraging juvenile owls. It appears that seasonally increasing insectivory in this study partially results from strategic nocturnal foraging by juveniles on terrestrial arthropods, such as ground beetles and crickets.

Evolutionary Mechanisms

Evolutionary mechanisms that could explain seasonally increasing insectivory are: 1) different post-breeding foraging habitat selection, and 2) a propensity for invertebrate prey because of reduced metabolic needs of post-breeding individuals compared to breeding owls (Gleason 1978, Lohoefener and Lohoefener 1982, Valdez 2003).

Foraging Habitat Selection - If Burrowing Owls forage opportunistically, employ similar foraging behaviours, and utilize similar habitats, then diets should not vary substantially between cohorts. However, rodent biomass is significantly greater in adult diets, songbirds are only substantial in female diets, and beetle biomass is significantly greater in the diet of juveniles than adult females. I do not know whether post-breeding adults foraged in habitats distinct from juveniles, but the dietary disparity between these cohorts suggests that either foraging habitat and/or prey selection varies with age in the late-season. Assuming that diurnally active prey are more likely to be preyed upon while owls occupy roosts, and daily movements at dusk indicate that nocturnally active prey are more likely to be preyed upon when owls are away from roosts in foraging sites, then the activity schedules of prey can provide clues that may help explain heterogeneous diets.

Diurnal prey groups include songbirds and invertebrates thermally constrained by lower critical temperatures, such as grasshoppers and darkling beetles. Songbirds are ubiquitous in the study area, but the infrequent use of this prey group suggests opportunistic foraging by owls on unwary songbirds. Except for songbirds, both the frequency and biomass of diurnal prey is relatively homogeneous among cohorts. Similar to nest burrows, diurnally inhabited roost burrows were typically located in native upland prairie. Because roosting habitat and prey use appears similar among cohorts, diurnal foraging appears opportunistic; however, because I did not quantify prey availability at late-season roost burrows, I am unable to confirm this deduction.

In contrast, dietary heterogeneity between adults and juveniles principally resulted from disparate biomass of nocturnally active prey, such as rodents and ground beetles. Because rodents inhabit specific habitats, the diversity of rodent species in adult diets suggests that these adults foraged nocturnally in a diversity of habitat types. For example, sagebrush voles inhabit xeric upland prairie (Carroll

and Genoways 1980), meadow voles are associated with mesic habitats with denser cover (Birney et al. 1976), and deer mice are, comparatively, habitat generalists (MacCracken et al. 1985, Sissons 2003). Deer mice are a principal species in Burrowing Owl diets (Sissons 2003) and were available in most prey-trapping grids, but juvenile owls did not use rodents available in nocturnal foraging sites. Seemingly, juvenile Burrowing Owls either have a preference for invertebrate prey or have limited proficiency hunting rodents.

Juveniles repeatedly foraged in habitats with greater arthropod abundances such as ephemeral wetlands, edge habitats, and heavily grazed and bare sites. Both nest site and adult male foraging habitat selection are similarly associated with ephemeral wetlands, habitat edges, and heavily grazed and bare areas (Gervais 2002, Green and Anthony 1989, MacCracken et al. 1985, Plumpton 1992, Sissons 2003, Thompson and Anderson 1988, Uhmann 2001, Warnock and Skeel 2002). These areas are minor components of the prairie landscape relative to upland prairie, suggesting that Burrowing Owls are attracted to particular habitat characteristics that are distinct from upland prairie.

Beetle abundances were greatest in ephemeral wetlands, ditches and edge habitats. Reasons that may explain this are: 1) beetle populations can respond positively to grazing (Sissons 2003), 2) beetles can be more active on bare areas because of the relative ease of movement compared to areas with denser vegetation (Bangert and Slobodchikoff 2004), and 3) habitat edges can be barriers to surface-dwelling arthropod movements that result in specialized arthropod aggregations (Duelli et al. 1990, French et al. 2001, Mader et al. 1990). Furthermore, because cryptic prey, such as beetles, are more easily detected on bare ground than in densely vegetated habitats, they are more available to owls in heavily grazed and bare sites.

Seasonally Reduced Metabolic Needs - In the same population studied here, Sissons (2003) describes breeding season diets dominated by vertebrate biomass

in both 1998 and 1999, but concurrent with increased consumption rates, vertebrate biomass decreases from 88% to 80-81% post-hatching. Increased post-hatching insectivory is also revealed by Errington and Bennett (1935), Green (1983), Gleason (1978), and Lohoefener and Lohoefener (1982), and this apparent dietary shift is concurrent with emergence of the adult female from incubation of thermally dependent eggs and owlets.

Unlike the adult male, which can forage many kilometres from the nest (Sissons 2003), females generally restrict their activity to the natal territory until fledging. Pre-fledging observations indicate that adult females foraging centrally in natal territories are primarily insectivorous, and that the adult males foraging nocturnally away from natal territories are primarily carnivorous (Pezzolesi and Lutz 1997, Poulin 2003). Although this suggests sexual differences, late-season adult male and female diets are comparable in this study, indicating that adults have similar niche-breadth once they are independent of the natal territory, as is suggested by York et al. (2002). It is possible that the foraging activities of adult males during the weeks when females are incubating eggs could deplete rodent abundances in the natal territories (Fautin 1946), precluding rodent hunting by the centrally foraging adult female after emergence.

Tracking post-breeding adult prey use shows that vertebrate biomass further decreases to 41-42% of late-season diet, which is still far greater than the 3% biomass in post-fledging juvenile diets. Increased post-breeding insectivory is concurrent with the independence of adults from the considerable food demands of the brood (see Gleason 1978), and the introduction of independent juveniles into the population. Principally insectivorous juveniles nocturnally foraged in areas with greater arthropod abundance and availability (i.e., reduced vegetation), demonstrating that vertebrate prey is not essential for individual sustenance. Because juveniles did not prey on rodents, even though deer mice were available in foraging sites, inexperience appears to be limiting juveniles to the readily captured prey (terrestrial beetles) instead of prey with the greatest biomass return

(rodents). The increased net return from rodent deliveries to the incubating female and owlets during breeding, the reduced food requirements of post-breeding adults, and in particular the apparent juvenile predilection for foraging on terrestrial arthropods (Butts 1973, Errington and Bennett 1938), all appear to contribute to seasonally increasing insectivory in Burrowing Owls.

CONCLUSIONS

Although these cohort specific diets represent a single year with extreme climate, seasonally increasing insectivory in Burrowing Owls appears to be more than a tactical response to arthropod population increases. Increasing insectivory also appears to be strategic, influenced by: 1) reduced food demands on post-breeding adults, 2) juvenile selection of nocturnal foraging habitats with greater arthropod abundances, and 3) juveniles may be able to capture invertebrates more readily than rodents. Although drought may have contributed to reduced rodent abundance, seasonally increasing insectivory was also likely influenced by increased effort collecting principally insectivorous juvenile pellets.

Future quantifications of Burrowing Owl dietary specialization should be operationally refined by: 1) the order of selection (Johnson 1980), 2) the age and sex of the owls, 3) the stage of the annual cycle, and 4) the foraging strategies (e.g., diurnal vs. nocturnal) and foraging behaviours (e.g., ground foraging vs. hoverhunting) employed. Juveniles appear to select nocturnal habitat for increased arthropod abundance and availability (i.e., third-order selection), but the prevalence of surface disturbances at these foraging sites suggests that this process may be influenced by anthropogenic disturbances. The procurement of individual prey items by juveniles may also be limited by hunting ability (i.e., fourth-order selection). Additional research in different geographical areas during seasons with more typical weather could determine if the pattern of seasonally increasing insectivory, in particular the extremely insectivorous foraging by juveniles, can be generalized.

CHAPTER 5

THESIS CONCLUSION

SUMMARY AND CONCLUSIONS

I tracked radio-tagged, post-breeding adult and post-fledging juvenile Burrowing Owls in southern Alberta, to assess juvenile survivorship, the effect of tags, and cohort specific late-season diets. This is the third study of juvenile survivorship in Canada, but the first in a relatively stable population and the second in comparatively expansive native prairie. The other survival estimates come from terminally decreasing populations in severely fragmented (Todd et al. 2003), and in similarly contiguous grassland habitat (Clayton and Schmutz 1999). This study was the second assessment of prey use specific to adult male and female owls, but the first description of juvenile Burrowing Owl prey and foraging habitat use.

Because birds often suffer high rates of mortality in their first year of life, excessive juvenile mortality could be limiting growth and recovery of endangered Canadian populations. Greater juvenile survivorship in this population compared to two terminally decreasing populations suggests that juvenile mortality is limiting population growth. Both breeding population (i.e., numerical) and recruitment (i.e., functional) increases one year after a summer of significantly higher juvenile survival (Todd et al. 2003) also provides evidence that juvenile mortality has a considerable effect on population demography. Because juveniles did not die for 6-7 weeks in a stable population in Idaho (King 1996), but most documented juvenile mortalities occured in the first 2-3 weeks of post-fledging independence in Canadian populations, early independence appears to be a critical period for juvenile survival prior to migration. Management actions that reduce fledgling mortality during periods of higher risk could prove beneficial to Canadian populations if these efforts result in increased recruitment.

Reduced survivorship of juveniles wearing necklace style tags raises serious questions about the efficacy of tagging Burrowing Owls with these markers.

Because these deaths could not be directly attributed to the tags, further research should assess tags effects, but this research would be better suited for captive owls in a breeding facility. Ideally, as technological improvements further reduce the size of tracking tags, and harnesses are better adapted to suit these owls, the negative impacts of tags will also be minimised.

An increased frequency of human-influenced mortalities is a consequence of habitat fragmentation, and fatal vehicle collisions are the majority of non-natural juvenile deaths in areas populated by humans (Todd et al. 2003, Clayton and Schmutz 1999). The evidence I have presented indicates that juvenile owls repeatedly foraged on roads because they were attracted to greater arthropod abundance, in particular ground beetles and crickets, and likely because arthropod prey was relatively more available on bare roads than when concealed by vegetation. Arthropod aggregations along roads are a likely explanation for the high incidence of fatal vehicle collisions across breeding range. Roads constructed in native prairie landscapes appear to act as ecological traps for owls foraging nocturnally by increasing prey availability and luring unwary juveniles into these areas, with associated increases in mortality risk.

Installing foraging perches beside roads has been suggested as a strategy to reduce the incidence of vehicular collisions with roadside foraging Little Owls in Europe (Hernandez 1988). Existing perches (fence posts) adjacent to roads did not preclude fatal collisions with juvenile Burrowing Owls in this study. Another strategy for reducing vehicle collisions is to install road signs requesting reduced vehicle speed near owl nests (Skeel et al. 2001). While this action beneficially increases public awareness of this issue, and reduced speed may effectively reduce collisions with more cautious adult owls (Illner 1992), reduced speed did not appear to prevent collisions with road-foraging juveniles in this study. Restrictions on crepuscular and nocturnal traffic during fledging could effectively reduce collisions, but may not be publicly accepted. Greater arthropod abundance and availability appears to be the incentive that draws ground-foraging juveniles

to roads. Either minimising new road construction in native prairie habitats, or reducing the attractiveness of roadside foraging sites by reducing arthropod abundance and simultaneously increasing arthropods in safe areas away from roads, will likely be the most effective conservation measures to reduce fatal vehicle collisions.

Although the ecology of economic prey (e.g., grasshoppers) is well researched, the ecology of other essential prey species, such as ground beetles and rodents, remains largely unstudied in the Canadian prairie. Better understanding of the ecological mechanisms that influence prey aggregations and reproduction could lead to conservation actions that augment owl productivity and survivorship.

Post-breeding adult male and female diets were similar in arthropod and vertebrate prey use, but the proportion of vertebrates in the late-season diets of this population is greatly reduced compared to the breeding season. The near exclusive insectivory of post-fledging juveniles likely affects this trend, therefore future descriptions of Burrowing Owl diets should endeavour to determine whether the pellets come from adults or juveniles.

I found the first incidence of horsehair worms consumed indirectly by Burrowing Owls inside parasitized arthropods. Horsehair worms consume arthropods internally and, although they are not believed to directly affect vertebrates, they remain undigested and reduce the energetic return when infected arthropods are consumed by owls. A better understanding of horsehair worm distribution and their effects on arthropod populations may ultimately provide insights for Burrowing Owl conservation.

Juvenile owls rarely preyed on deer mice that were available in nocturnal foraging sites; instead they preyed almost exclusively on arthropods. If insectivory is a common post-fledging foraging strategy for juveniles, conservation actions that increase terrestrial arthropod abundance and availability away from roadways

could be implemented to decrease starvation and collisions. Furthermore, because juveniles principally forage on insects, they may be more susceptible to secondary contamination in agricultural landscapes that are treated with biocides. Current regulations restrict spraying of some insecticides in the immediate vicinity of nest sites, but foraging juveniles are typically dispersed from these sites. Better understanding of late-season foraging in agricultural landscapes may reveal conservation strategies that could prevent the ingestion of insecticides by foraging juveniles.

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APPENDIX A. The relative abundance of beetles captured in 248 pitfall traps in foraging, 248 pitfall traps in range-control, and 108 pitfall traps in road-control prey-trapping grids.

COLEOPTERAN FAMILY Carabid Tribe Species	Total Beetles	Relative Abundance (# captured/# traps)		
		Foraging	Range-control	Road-control
CARABIDAE (ground beetles)	664	1.778	0.432	1.176
Agonini	2	0.008	0	0
Agonum cupreum Dejean	2	0.008	0	0
Amarini	191	0.008	0	0
Amara apricaria Paykull	2	0.008	0	0
Amara carinata LeConte	6	0.021	0.004	0
Amara confusa LeConte	12	0.029	0.021	0
Amara obesa Say	158	0.140	0.193	0.713
Amara quenseli Schonherr	13	0.008	0.021	0.056
Bembidiini	1	0.004	0	0
Bembidion nitidum Kirby	1	0.004	0	0
Harpalini	365	1.325	0.111	0.148
Bradycellus congener LeConte	1	0.004	0	0
Harpalus amputatus Say	344	1.280	0.103	0.074
Harpalus somnulentus Dejean	15	0.037	0.008	0.037
Harpalus ventralis LeConte	3	0.004	0	0.019
Piosoma setosum LeConte	2	0	0	0.019
Lebiini	74	0.123	0.053	0.176
Calleida viridis amoena LeConte	1	0	0.004	0
Cymindis interior Lindroth	12	0.016	0.008	0.056
Cymindis plenipennis LeConte	49	0.107	0.041	0.120
Microlestes curtipennis Casey	12	0.004	0.025	0.046
Pterostichini	58	0.086	0.016	0.046
Pterostichus corvus LeConte	28	0.103	0.012	0
Pterostichus melanarius Illiger	1	0.004	0	0
Pterostichus scitulus LeConte	29	0.082	0.016	0.046
Scaritini	13	0.025	0.012	0.037
Pasimachus elongatus LeConte	13	0.025	0.012	0.037
CINCINDELIDAE (tiger beetles)	50	0.053	0.045	0.111
Cincindela nebraskana Casey	36	0.053	0.045	0.111
Cincindela purpurea LeConte	14	0.016	0.016	0.056
CURCULIONIDAE (snout beetles/weevils)	61	0.053	0.066	0.296
Unidentified weevils	61	0.053	0.066	0.296
DERMESTIDAE (dermestid beetles)	3	0.008	0.004	0
Thanatophilus lapponicus Herbst	3	0.008	0.004	0
HISTERIDAE (hister beetles)	3	0.008	0	0.009
Unidentified hister beetles	3	0.008	0	0.009
SILPHIDAE (carrion beetles)	8	0	0.033	0
Nicrophorus spp.	8	0	0.033	0
TENEBRIONIDAE (darkling beetles)	107	0.235	0.128	0.176
Acidopsis polita Say	6	0	0.012	0.028
Caelocnis dilaticollis Mann	1	0.004	0	0
Eleodes extricata Say	1	0	0.004	0
Eleodes hispilabris Say	37	0.058	0.062	0.074
Eleodes obsoletaus Say	1	0	0.004	0
Eleodes opaca Say	14	0.021	0.008	0.065
Eleodes tricostata Say	3	0.008	0.004	0
Embaphion muricatum Say	2	0.004	0.004	0
Melanastus ater Lec	50	0.144	0.045	0.037
Total	944	2.26	0.78	1.90